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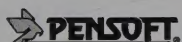# in the Northeast
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by

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Edited by

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TRANSLATOR'S PREFACE

The book *Overwintering and Cold-Hardiness of Ants in the Northeast of Asia* by D. I. Berman, A. V. Alfimov, Z. A. Zhigulskaya and A. N. Leirikh is an English translation of a monograph of the same name published in Russian in 2007 by the Moscow publisher KMK Scientific Press. The Russian version was edited by the well-known Russian myrmecologist Professor Gennady M. Dlussky of Moscow University, and this English version was edited by the British entomologist Robert B. Angus, who has been in Russia several times and happens to have some personal experience of the extreme conditions of northeastern Asian climate discussed in this book. Arkady V. Alfimov, one of the authors, checked the entire English version of the text and consulted the translator and the English editor on special terms and other issues that had to be clarified.

The scope of the book is rather broad: it includes general and local aspects of the study area's peculiar climate, characteristics of the ant species living in the area (including their nest structure, overwintering stages, and geographical and spatial distribution), and the results of numerous experiments that revealed the parameters of cold-hardiness in thousands individual ants from dozens of nests. Preparing a monograph of this scope was possible thanks to the different fields in which the four authors are specialised: D. I. Berman, Chief of the Biocoenology Laboratory at the Institute of Biological Problems of the North in Magadan, is an ecologist and biogeographer, A. V. Alfimov is a microclimatologist, Z. A. Zhigulskaya a myrmecologist, and A. N. Leirikh is a physiologist earlier educated in physics.

In the literature available (both in Russian and in English), there are but a few large-scale studies of insect overwintering and cold-hardiness, and this book is probably the first one where the cold-hardiness of all the species from a particular taxonomic group living in an area with long and severe winters is studied in detail, based on large amounts of material collected in the field and experimented upon in the laboratory. This is one thing that is unique about the book, but there are at least two more unique things about it: the choice of the taxon, and the study area. Ants are the only social insects capable of long-term surviving in the extreme winter cold of the Northeast of Asia. The study area itself is also unique: being not far from, and only slightly warmer in winter than the very coldest area of the Northern Hemisphere, the so-called Pole of Cold in northeastern Yakutia, it is also often affected by strong winter winds (rare in northeastern Yakutia), redepositing the snow and

creating in the soil, where ants are overwintering, conditions sometimes even more severe than under the snow cover in northeastern Yakutia. What makes the overwintering of ants in much of northern Asia, including the Northeast, an especially hard endeavour is the continuous permafrost, which makes it impossible for ants to build the wintering chambers of their nests as deep as they can in other regions.

Permafrost and harsh winter cold of the area make it ideal for studying the overwintering and cold-hardiness of animals, but these same conditions make the process of the study extremely difficult and labour-consuming. It is all the more difficult because the area is sparsely populated; settlements are few and separated by huge distances, roads rare and often barely (if at all) passable, many localities can be reached only by helicopter. The Kolyma region is infamous for housing in Stalin's time the cruellest forced-labour camps, where many thousands of innocent people died of cold and starvation. Years of hard fieldwork in the severe climate of that region stand behind this detailed study. To have a laboratory for working all the year round in the mountains of the Upper Kolyma, D. I. Berman and his colleagues from the Institute of Biological Problems of the North had to build in the mountains of the Upper Kolyma the Aborigen Field Station, 500 km from the city Magadan on the coast of the Sea of Okhotsk. This station enabled much of the work that made this book possible to be carried out.

The Russian version of the book was warmly received by myrmecologists and ecologists. It was reviewed by the myrmecologist Elena Fedoseeva, Zoological Museum of Moscow State University, in the leading journal on zoology published by the Russian Academy of Sciences, *Zoologicheskii Zhurnal*. Her review highlighted the novelty of the results and the huge amount of work required from the authors (and those who assisted them) to obtain these results. The reviewer also noted that the mass of scientific information currently accumulated in ecology leaves many problems unsolved because of the extreme specialization of researchers and lack of cooperation between them. The complex nature of the ecological problems discussed in the book required the collaboration of specialists in different fields, and the book shows how productive such collaborations can be.

The publication of this monograph in English will make it accessible to many more readers. The English language has long established itself as the international language of communication and of science, a place occupied until a few hundred years ago by Latin. Scientific results obtained in Russia are, unfortunately, underrepresented in English-language scientific literature. The Iron Curtain, which divided political systems, hindered not only the travelling of people, but also the spreading of scientific knowledge and ideas. Publishing in English was viewed with suspicion and rarely encouraged in the Soviet Union. Another big obstacle was inadequate knowledge of English, which was usually far from fluent even among members of the Soviet academia. Some achievements of Soviet science remained known largely only to Soviet scientists and their colleagues from other socialist countries and not to the whole international scientific community. Fortunately, the situation seems to

be changing for the better. Russian scientists publish their works in English more and more often. For instance, a few years ago (in 2007) another monograph discussing ants, Zhanna Reznikova's study on animal intelligence (*Animal Intelligence: From Individual to Social Cognition*) was published by Cambridge University Press. The publication of the English version of *Overwintering and Cold-Hardiness of Ants in the Northeast of Asia* is another step forward in making the work of Russian scientists known to their colleagues worldwide.

Making the content of this book known outside Russia is all the more important since the results presented in the book could not be obtained in any other country, simply because in no other country winters are as severe. Large areas of Canada and USA's Alaska also have very cold winters, but the winter temperatures of the parts of northeastern Asia with most strongly continental climate are still unmatched by any other place on Earth, with the exception of the Southern Hemisphere's (and the planet's) Pole of Cold in Antarctica—but no ants are native to Antarctica.

The results obtained by D. I. Berman and his team are diverse in nature and will be of interest not only to myrmecologists, but also to ecologists and ecological physiologists, as well as climatologists. The following aspects of ant overwintering and cold-hardiness are elucidated in the book: the bionomics of ant overwintering (including the habitat distribution, nest structure and overwintering stages of each species found in the area); the microclimate and temperature conditions of the overwintering of each species; and the physiological parameters related to cold-hardiness, measured in samples of each species (including supercooling points, freezing points, long-term tolerable temperatures, and levels of cryoprotectant substances in the haemolymph). The study of all these aspects required many years of Herculean labours. Sitting in a warm room in Moscow, where I write this preface, with moderately cold weather outside (only around −15 °C, rather cold for Moscow in January, but quite warm compared to the Upper Kolyma, where about −35°C is the average for January, and −50 °C is not uncommon), it is hard to imagine the conditions in which fieldwork had to be done in the environs of the Aborigen Station. As if cutting heavy cubes containing ant nests from the frozen ground covered with snow and bringing them to the station was not enough, the authors and their helpers had to put these nests with the ants they contained into a cold laboratory room, to protect the ants from heat shock, which could spoil the results of subsequent experiments. It was in this cold room, at temperatures as low as −10 to −15 °C, that individual ants had to be extracted from the nests and sorted out for experiments.

These hard labours allowed the authors to obtain really interesting results. The ants found in the study area belong to four genera (*Myrmica, Leptothorax, Camponotus* and *Formica*). Species of these genera differ in their strategies of adaptation to overwintering at low temperatures. *Leptothorax* and *Camponotus* display extremely low values of supercooling point. (Unlike some other overwintering invertebrates, but like all vertebrates, ants are unable to survive freezing, i.e. formation of ice crystals in cells and bodily fluids; to protect themselves from freezing under sub-zero

temperatures, they have to stay in the supercooled state, cooled but not frozen; supercooling point is the temperature below which the supercooled state is no longer possible). Species of the genus *Myrmica* and one of the several species of *Formica* (*F. gagatoides*) have higher supercooling points, but their supercooled state is more stable, compared to that of *Leptothorax* and *Camponotus*, and can be maintained longer; these species build their nests in localities with a rather deep permafrost table, where wintering chambers can be positioned far from the surface and the temperatures in them are not so low and more stable than closer to the surface. The other species of the genus *Formica* are the least cold-hardy; they build their nests only in habitats with winter conditions as favourable as possible; fluctuations of winter weather probably repeatedly wiped out populations of these species over large areas, resulting in long-term changes in their geographical ranges. This diversity of adaptation strategies is surprising, but it was convincingly shown by experiments with large sample of ants of each species.

Although the conditions of the Northeast of Asia require effective adaptations to overwintering at very low temperatures, it is probably rather lack of summer heat than excess of winter cold that causes the depletion of the ant fauna towards the north and the disappearance of them farther, on the tundra. Short summers with relatively low temperatures do not allow ants of most species to complete their life cycle in one year and overwinter as adults. Only a few species are capable of prolonging the life cycle to more than one year and overwintering for the first time as larvae.

The monograph contains plenty of information on the cold-hardiness and overwintering of ants, but the subject is still far from closed, and several further research objectives are outlined in the book. One of them is the study of cold-hardiness in ants that overwinter at even lower temperatures than those in the Kolyma region, for instance in northeastern Yakutia (the Pole of Cold), Transbaikalia and the Upper Amur valley, where the snow cover is often very thin and fails to insulate the upper layers of the soil from the cold winter air. Time and further experiments will show whether the adaptive strategies of ants at the very limit of their potential cold-hardiness are different from those found in the extreme conditions of the Kolyma region. The monograph sets an example and provides a firm foundation for further studies of overwintering and cold-hardiness, not only in ants, but also in other invertebrates living in areas with extremely cold winters.

PYOTR PETROV

PREFACE OF THE EDITOR OF THE RUSSIAN EDITION

More than half the area of Russia and large portions of North America (Alaska, Canada) are covered with permafrost. These territories are inhabited by thousands of invertebrate species, but the actual overwintering conditions, physiological mechanisms, and behavioural features enabling them to withstand low temperatures are known only in a few of them.

Studies of cold-tolerance in animals of Russia were started at the end of the 19th century by P. I. Bakhmetyev, who showed that surviving in a state of anabiosis is only possible if tissue fluids remain supercooled. In the 1930s, N. I. Kalabukhov published the brilliant book *Animal Dormancy*, which inspired new studies of the hibernation of animals in their natural environments. In the Soviet Union, these studies were especially intense in the 1950s–1970s, resulting in the monographs *Fundamentals of Insect Cold-Tolerance* by R. S. Ushatinskaya (1957) and *Essays in Cryobiology* by L. K. Lozina-Lozinsky (1972). Since the 1960s, cold-tolerance has been the subject of detailed studies in Canada, Japan and Scandinavia. In contrast, in the Soviet Union such studies virtually ceased from the mid-1980s and were continued only by a small group of scientists headed by D. I. Berman, Chief of the Biocoenology Laboratory at the Institute of Biological Problems of the North, Far Eastern Branch, Russian Academy of Sciences. Following the interesting publications of these researchers over many years, we have finally prepared a monograph summarizing their work on the biology of ants under extreme northern conditions.

It should be emphasized that so far most of the publications have only discussed the issues of animal overwintering in the temperate climatic zone, whereas the peculiar features of cold-hardiness in the invertebrates of the vast areas with very cold winters are clearly in need of more studies. As for the works carried out in Antarctica and Svalbard, they include detailed results of research on the physical and chemical mechanisms of cold-tolerance in only a few species, whereas the ecology of overwintering animals remains almost entirely unknown.

These circumstances highlight the current importance of the present monograph, summing up 30 years of studies on the ecology and physiology of ants under extreme northern conditions, virtually at the northern boundaries of their geographical distribution. It is noteworthy that the book is written by a group including two zoologists (D. I. Berman, Z. A. Zhigulskaya), a microclimatologist (A. V. Alfimov) and an ecological physiologist (A. N. Leirikh). At this time of nar-

row expertise, such a complex and high-quality work could only be produced by a well-coordinated group of researchers, this book being another evidence of this. Such an approach has allowed the authors to appreciate the entire range of strategies—not only physical chemical and physiological, but also ecological, ethological and others—of adaptation to spending the entire life cycle or some of its stages at low temperatures of the environment. The authors correctly emphasize that within this approach the most promising objective is the study of widely distributed species under extreme conditions, where the adaptive potential of the organism is especially strikingly revealed. In the northern continental areas, animal species of diverse origins and with different ecological and physiological potentials coexist due to the vast range of microclimatic conditions.

The study was carried out mostly at the Aborigen Field Station in the upper reaches of Kolyma River and some other places in the Magadan Region, Russian Far East. The winter climatic parameters of this area are close to those of the "Pole of Cold" in northeastern Yakutia, where even in the uniquely "warm" habitats winter temperatures never exceed −9 °C, whereas background temperatures in near-surface layers of the soil in winter usually drop as low as −45 to −50 °C in snowless areas (which is close to the lowest air temperatures) and as low as −20 to −25 °C in areas covered with thick snow.

The choice of the study object is not arbitrary either: ants are perfect models for studying many phenomena, including cold-hardiness in natural environments. Cold-hardiness is usually studied in the laboratory, by collecting individual invertebrates in autumn and observing their overwintering under conditions the experimenter believes to be as close to natural as possible. The overwintering of ants, however, can be studied in their natural environments. The authors marked ant nests with long stakes in autumn and in winter cut out frozen monoliths containing the nests, brought them into a cold laboratory room and distributed small portions of ants in weighing bottles, subsequently using them for experiments as required. Certainly, this technique demanded considerable efforts on the part of the researchers possible only through great enthusiasm and teamwork. But their labours seem to have been fully rewarded by the results obtained. This monograph is virtually the first work in the world providing a comprehensive picture of the life of ants under extreme northern conditions.

Like most works of this kind, the monograph begins with descriptions of the landscapes and climates of the study area. There is, however, an important distinction. Zoologists normally limit themselves to data from reference books and other literary sources, whereas this work provides much original data on the microclimate of particular localities, helpful for better understanding the conditions under which ants live in particular habitats. Now we know for certain what the thermal regime is in the "ecologically active layer" (i.e. the soil and the inhabited upper part of the underlying grounds) near the Pole of Cold. It should be emphasized that although permafrost is extremely widespread in the forest zones of Eurasia and North Amer-

ica, there are no special studies on the living conditions of the soil-dwelling animals of such areas. The data of the authors on conditions occurring in different types of permafrost ("dry" and icy) are of special interest in themselves, because they can be used for analysing the distribution of any organisms inhabiting the permafrost areas not only in the subarctic Northeast Asia, but also across much of Siberia and North America.

As a myrmecologist, above all I expected getting from this book new data on ants, and my expectations were fulfilled. The monograph contains unique data on the bionomics of particular species in subarctic climate at the northern boundaries of their ranges. All that was known to science on this subject was the bionomics of ant species in Scandinavia, at latitudes close to those studied by these authors (60–70° N), but with immeasurably warmer climate, and thus, in a way, less interesting. This study provides information on the geographical distribution, habitat allocation, nest-building characteristics and seasonal dynamics of ants inhabiting northeastern Siberia. Of special interest are the data on the structure of ant nests, based on materials the collection of which required the both physically laborious and simultaneously accurate work of excavating the nests both in summer and in winter.

The chapter *Ant Cold-Hardiness and Its Determining Physiological and Biochemical Factors* makes the entire study especially valuable. It provides the first quantitative data on the cold-hardiness of ten species of ants from four genera (*Myrmica, Leptothorax, Camponotus* and *Formica*) most abundant in the study area. The physiological mechanisms behind this hardiness are shown.

Thus, the book presents an integral picture: the regional geographical distribution, habitat allocation, nest organization, overwintering family composition, thermal conditions in nests, reactions to low temperatures (supercooling points, freezing points, lowest tolerable temperatures) and seasonal changes of cryoprotectant concentrations were studied in one taxonomic group in one really cold area. This picture is valuable by itself, even without any conclusions. The generalizations made by the authors are, however, both important and interesting. The authors have convincingly shown the multidimensionality of adaptive strategies of survival in the extreme north. In some species the ability to exist in such an environment is determined mainly by their strong physiological cold-hardiness, and in some their lack of physiological capacities is compensated by choice of appropriate habitats with specific microclimate or by peculiar structure of nests. The conclusion that each of the studied species has its own specific adaptive strategy is somewhat unexpected, but is convincing. The authors believe that this fact makes it rather unlikely that a general strategy of adaptation to cold (including its physiological/biochemical and behavioural aspects) will ever be revealed, at least in ants. It would be extremely interesting and important to test this pessimistic conclusion with other animal taxa (no such data are available in the literature at present).

The analysis in this book explains the causes of ant fauna depletion at the northern boundaries of ranges and shows the diversity of these causes. Only a small

proportion of the species in the Northeast of Asia are free from the pressure of low winter temperatures, and in these species the northern limits of distribution are determined by summer conditions. The monograph shows, however, that even in the extreme north biotic relations still play an important part in the genesis of fauna.

A great merit of this book is its detailed description of the methods of field and laboratory work, which can be used in the future by other researchers. One of the accomplishments of the authors is, undoubtedly, the development of techniques for estimating the parameters of cold-hardiness in individuals overwintering in their natural environments. These techniques will guard against mistakes in adjusting the conditions for winter maintenance of animals in the laboratory. This is particularly important since the authors have revealed very rapid changes in physiological parameters, including the lower supercooling temperatures, in all the species under changing conditions.

The monograph is certain to appeal not only to myrmecologists (in this respect it is unique in the abundance of facts it provides on the ecology of particular species), but to all biologists interested in the cold-hardiness and survival of animals under the severe conditions of the subarctic climate.

To conclude this brief preface, I would like to note that the Biocoenology Laboratory in Magadan is currently the only research unit in Russia studying the winter ecology of invertebrates. I wish them every success in their future difficult and exciting work and hope that this book will attract new researchers to work in this field.

PROFESSOR GENNADY DLUSSKY

INTRODUCTION

The main feature common to all the climates of Russia is the cold winter. The proportion of areas with positive temperatures in winter is negligible, and permafrost covers almost 60% of the country. In the northern parts of North America—Canada and Alaska—the situation is similar. Thousands of invertebrate animal species winter every year in these areas. The actual conditions of overwintering and mechanisms of cold-resistance are known in only a few dozen of these species. The current knowledge of the phenomenon, unfortunately, fails to match its scale.

Physiological, ecophysiological and ecological studies of this extreme aspect of invertebrate animal life are developing and their scope is becoming broader. At the beginning of the last century studies of how animals withstand low temperatures were focused on anabiosis (works of P. I. Bakhmetyev, P. Yu. Schmidt), and in the middle of the century such studies were largely oriented towards agricultural pest control and cryopreservation of tissues and organs. The most important landmarks in the development of these approaches were the monographs *Fundamentals of Insect Cold-Tolerance* by R. S. Ushatinskaya (1957), *Essays in Cryobiology* by L. K. Lozina-Lozinsky (1972) and *Ecology and Physiology of the Colorado Potato Beetle* by R. S. Ushatinskaya & G. G. Yirkovsky (1976). Cryopreservation became in due course a separate, successfully developing discipline, focused mostly on applied objectives. The cold-hardiness of invertebrates was studied for some time at Leningrad State University, at the University of Tartu, and at the Institute of Animal Evolutionary Morphology and Ecology (Moscow). A conference on cold-tolerance of insects and acarines was held in Tartu in 1971, and the monograph *Cold-Hardiness of Insects* by E. E. Merivee was published in 1978.

The results of these works largely determined the development of this approach in the following decades. For instance, the connection between cold-tolerance and the presence and profundity of diapause was revealed in some invertebrate taxa (Merivee, 1972; Ushatinskaya, 1980), the existence of nonspecific cold-tolerance related to particular stages of ontogeny and diapause (Merivee, 1978; Ushatinskaya & Ivanchik, 1974; Luik, 1975; Ushatinskaya &

Chesnek, 1974) and differences in cold-tolerance between insect populations from different geographical localities (Pantyukhov, 1956, 1964; Hansen, 1978) were shown. The characteristics of cold-hardiness were described for many invertebrate species (Hansen, 1980a), and the list of species surviving winter in their natural environments in a frozen state was enlarged (Hansen, 1980b). The criteria of cold-hardiness were developed and improved (Merivee, 1978), along with studying facilities (Goryshin, 1966) and methodological techniques (Merivee, 1970; Kuusik, 1971) for acquiring adequate results and interpreting them unambiguously. The most excellent summation of this period of studies was the publication of the book *Hidden Life and Anabiosis* by R. S. Ushatinskaya (1990). Work in this field virtually ceased in the former USSR by the mid-1980s.

Meanwhile, studies of cold-hardiness started developing rapidly in Canada, Japan and Scandinavia since the 1960s. The first international meeting on different aspects of invertebrate cold-hardiness was held in 1982 in Oslo. The same year marked the publication of the first part of a bibliographic checklist on the physiology and biochemistry of low-temperature tolerance in insects and other terrestrial arthropods (Baust et al., 1982), containing over 500 references. In 1986 the second part of the checklist with over 150 references was published (Lee et al., 1986). Finally, in 1991 a group of 39 authors published the monograph *Insects at Low Temperature* edited by R. E. Lee & D. L. Denlinger (1991), which reflected the state of the discipline and became the reference book for all who study cold-hardiness. In this monograph, the basic notions were formulated and the general principles of insect cold-hardiness, as well as the properties and balance of water and the biochemistry of cryoprotectants and specific proteins important for providing tolerance to negative temperatures were discussed. Much attention was paid to the adaptations of particular species, to groups of terrestrial and aquatic Arctic invertebrates, as well as to the practical applications of the knowledge on cold-hardiness to cryopreservation of cells, tissues and entire insect organisms, to pest control, bee overwintering and silkworm breeding.

All these areas were successfully developed over the last 15 years by many researchers, including the unofficial group that authored the above-mentioned monograph. Reviews were regularly published, not only on the key elements of the physiology of cold-hardiness, such as water balance (Danks, 2000; Block, 2002), ice nucleation (Lee & Costanzo, 1998; Zachariassen & Kristiansen, 2000; Lundheim, 2002), inorganic ions (Zachariassen et al., 2004), low-molecular cryoprotectants (Kostal et al., 2001, 2004; Wharton, 2003; Fuller, 2004; Williams et al., 2004) and antifreeze proteins (Davies et al., 2002; Duman et al., 2004), but also on the state of the field in general (Somme, 1995; Denlinger & Lee, 1998; Bale, 2002; Danks, 2004, 2005; Turnock & Fields, 2005). The

biochemistry of cryoprotectants (Muise & Storey, 1999, 2001), the regulation of metabolic rate (Storey & Storey, 2004) and the mechanisms of cold stress damage and repair (Joanisse & Storey, 1998) were studied. Cold-hardiness featured prominently in programs of the regularly held international workshops on the ecophysiology of invertebrates (for materials of the 2nd, 3rd and 4th workshops see Proceedings…, 1996, 1999, 2002 in *European Journal of Entomology*).

Many authors have discussed the possible physical-chemical mechanisms of cell and organism survival both in supercooled and frozen states, using data on membrane condition, free and bound water etc. (Lozina-Lozinsky, 1973; Somme, 1967; Asahina, 1966; Salt, 1957, 1959, 1962, 1966a; Baust & Morrissey, 1975; Ring & Tesar, 1981; Poinsot-Balaguer & Barra, 1983; Yi & Lee, 2003; Worland et al., 2004; Ozernyuk, 2000). Works on the cold-hardiness of invertebrates are still mostly inventory-like: temperature parameters of cold-hardiness are measured and mechanisms of cryoprotection are explored.

Unfortunately, ecological aspects of cold-hardiness are nothing like so well elucidated. Barely a few dozen such studies are available. Most of them either treat the adaptations of invertebrates overwintering under conditions with known and easy to measure temperature parameters: in tree trunks or even in the air above the snow surface (Madrid & Stewart, 1981; Ring & Tesar, 1980; 1981; Lee & Zachariassen, 2006), or deal with the "exotic" Antarctic insects (Baust & Lee, 1981; Block, 1981; Worland, 2005; Block & Zettel, 2003; Block & Convey, 1995, 2001). For instance, the gall midge *Eurosta solidaginis*, often overwintering above the snow line in the third instar larval stage, has become a model subject for such studies. Many dozens of works were published on its ecology, physiology and biochemistry (see Danks, 2005; Williams & Lee, 2005; Williams et al., 2004; Fuller, 2004; Irwin & Lee, 2002; Yi & Lee, 2003). A series of papers describes the ecology of the arctic moth larva *Gynaephora groenlandica* (see Danks, 2005; Bennett et al., 1999, 2003). Collembola are the taxon with the most thoroughly known taxonomic composition, set of life forms and diverse aspects of ecology and cold-hardiness (Somme, 1976, 1978, 1981, 1999).

Most works on the cold-hardiness of invertebrates naturally deal with species occurring in areas of the Northern Hemisphere with temperate climates, whereas studies of the peculiarities of invertebrate cold-hardiness in areas with very cold winters, marked by the distribution of permafrost, are virtually missing.

Yet it is under the extreme conditions of regions with continental climates, where microclimatic differentiation is strongly pronounced and seasonal ranges of temperatures are wide, that the adaptive capacities of organisms vividly manifest themselves. Communities and species of animals with different physiological requirements and adaptive strategies exist side by side in small territories of continental areas due to huge microclimatic contrasts. This is often the case,

for instance, with relict steppe species, probably preserved since the Late Pleis-tocene (Kholodnye..., 2001), and tundra species, penetrating through forest-tundras. Transitional versions of habitats allow observation of the changes in species abundance (as well as the condition of families in ants) depending on the compliance of physiological capacities, e.g. parameters of cold-hardiness, with thermal conditions.

Some more advantages of studying adaptive strategies in cold continental areas could be named. However, long series of works carried out in Antarctica and Svalbard were focused mostly on studying in detail the physical-chemical mechanisms of cold-hardiness of a small number of species and not on the ecol-ogy of overwintering animals. We believe that the latter should include studies not only of physical-chemical and physiological, but also of ecological, ethologi-cal and other systems and strategies of adaptation to spending the life cycles or some of their stages at low temperatures of the environment. The complex of adaptations is most thoroughly known in the Antarctic oribatid mite *Alaskozetes antarcticus* (Block & Convey, 1995) and in the Antarctic springtail *Cryptopygus antarcticus* (Worland & Block, 2003), as well as in the Arctic springtail *Onychi-urus arcticus* (Block, 2002; Worland & Block, 2003).

Since the early 1980s the Biocoenology Laboratory of the Institute of Biological Problems of the North, Far Eastern Branch, Russian Academy of Sciences, has been studying the ecology of overwintering invertebrate animals, mainly in the Upper Kolyma basin (Fig. 1) at the Aborigen Field Station. The station (Alfimov, 1986; Biologicheskaya stantsiya..., 1993) is situated in the Bolshoy Annanchag Range, part of the Chersky mountain chain. The winter climatic parameters of this area are close to those of northeastern Yakutia, the universally recognized "Pole of Cold" of the Northern Hemisphere. It is shown below that the soil temperature in this area never rises above −9 °C in winter even in uniquely "warm" habitats, whereas background temperatures in near-surface soil layers in winter usually drop as low as −45 to −50 °C in snowless places (which is close to the lowest air temperatures) and as low as −20 to −25 °C in areas covered with thick snow.

Detailed knowledge, on the one hand, of the ecology of a number of abun-dant species of invertebrates (not only ants), and on the other hand, of the mi-croclimatic differentiation of the territory, including the real temperature condi-tions of wintering, stimulated the study of the capacities of animals to withstand low temperatures. Initially we planned to employ data on the cold-hardiness of ants, earthworms, grasshoppers, click beetles, myriapods, terrestrial molluscs and some other taxa, only partly published at present, exclusively for revealing the factors that control their spatial distribution (both biotopic and geographic) in the Northeast of Asia. Later the studies of role played by cold-hardiness in

Fig. 1. Location of the field station and the area of station-based studies (shown in red).

the adaptive strategies of invertebrates developed into an independent branch of the work carried out by our laboratory.

At present the most thorough data have been collected on ants. In most communities of the Upper Kolyma ants occupy one of the top positions in abundance, and in some habitat types, where the nests of the ant *F. exsecta* are very common, ants are prevalent among the soil macrofauna also by biomass. The dominant positions of ants and their high absolute abundance in subarctic ecosystems, indicating their success, appear rather unexpected, since the Upper Kolyma is close to the boundary of the range in most of the species abundant in this area (Zhigulskaya & Berman, 1975). Almost all of these species have their individual pattern of landscape and habitat distribution, including altitudinal zonal; they also display considerable variance in abundance, nest structure etc. Ants overwinter at different depths, in most cases reflecting the stereotypical building behaviour of their species.

The abundant species of the area belong to four genera having, as it appeared, different physiological and biochemical mechanisms of cold-resistance. The great number of individuals in the nests and the possibility to mark the positions of nests in autumn for finding them at any time in winter give the experimenter a unique opportunity to have always at hand the required amount of material from localities with the same environmental and overwintering conditions. All these facts were strong reasons for us to choose ants for in-depth study as an extremely convenient model taxon.

Most of the material of this book was collected from 1976 to 1985. The small number of studies of ant cold-hardiness published by our colleagues in the 1970s and 1980s has still remained small. The available information on the more than 250 species of ants of the former USSR included data on the lowest supercooling temperature only for a few species, measured mostly in the temperate zone (Kipyatkov, 1971; Maavara, 1971). The main conclusion of these works was that ants were unable to survive freezing and displayed cold-hardiness, estimated by the above-mentioned parameter, redundant for dwelling in the temperate zone. Only *Formica aquilonia* was studied relatively in detail: its seasonal changes of the lowest supercooling temperature were recorded, mortality caused by exposure of different duration to sub-zero temperatures was determined, and the content of reserve and cold-protective compounds was measured at different time of year in ants from different parts of the nest (Hansen & Wijk, 1981a, 1981b; Maavara, 1983). Equally detailed was the study of the cold-hardiness of *Formica polyctena* in Germany (Erpenbeck & Kirchner, 1983). In addition to the above-mentioned, a small series of papers treated two closely related species, *Camponotus obscuripes* and *C. herculeanus*, describing their two-stage freezing (of crop content and of tissues separately) and determining their lowest supercooling temperature and their glycerol concentrations (Ohyama & Asahina, 1972; Somme, 1964; Takehara & Asahina, 1960; Tanno,1962). Recently published works include studies of cold-hardiness in *Leptothorax* cf. *canadensis* (Heinze et al., 1996) and in *L. acervorum* (Heinze et al., 1998) and of the overwintering and cold-hardiness of *Camponotus pennsylvanicus* in Virginia, USA (Fell, 1992). A small series of papers treats the cold-hardiness of the red imported fire ant (*Solenopsis invicta*) in view of its invasion threat and possible counter measures (for review, see Taber, 2000; Quarles et al., 2005; James et al., 2002).

Particularly noteworthy is the work that was probably the first Russian publication on the overwintering of ants: prepared by the patriarch myrmecologist P. I. Marikovsky (1965), it contained very accurate observations of the behaviour and ecology of *Formica rufa* throughout the course of its overwintering.

The works mentioned are virtually all the publications on the cold-hardiness of ants that exist in the world (with the exception of our own works: Berman et

al., 1980–1987; Berman & Zhigulskaya, 1995a, 1995b, 1995c, 1996b; Leirikh, 1985, 1989).

The second reason for preparing this monograph was the considerable amount of data we collected on the spatial distribution, biology of development and ecology of ants in the Northeast of Asia. Moreover, there was no information in the literature on these aspects of the ants of our study area.

Finally, the third reason was the fact that at present there is not a single monograph in the world providing an integrated picture of the overwintering in a sample of species from any group of insects in any particular area with really cold winters.

The study included three large sections reflected in this monograph. Firstly, the geographical distribution of ants in the Northeast of Asia, their detailed landscape and habitat allocation in the upper reaches of the Kolyma, the characteristics of their nest structure and of the localization of the individuals overwintering in the nests were determined ascertained. Secondly, the patterns of winter soil temperatures and, against this background, the temperature conditions of the overwintering of ants were studied. Thirdly, the physiological resistance of ants to cold temperatures and the biochemical mechanisms providing this resistance were ascertained within the limits of our available methods of analysis. Seasonal changes of these parameters were studied in most species.

We have collected data on the geographical distribution of ants (along with data on other animals) in the Northeast of Asia since 1973. Our routes covered the Oymyakon Depression, the valley of the Indigirka from the villages of Ust-Nera to Predporozhny, the Ebe and Inyali landscape units, the environs of Tyubelyakh and Khonnu (Moma); the valley of the Nera River, right-hand tributary of the Indigirka, from its head to its mouth; the valley of the Moma River from the upper reaches of one of its sources, the Buordakh River, to the mouth. In the Kolyma, the valleys of its sources (Ayan-Uryakh, Berelekh, Kulu) and the valley of the Kolyma itself over its entire length from the junction of the Kulu and the Ayan-Uryakh down to the mouth. Ants were also collected along the highways Magadan–Susuman–Ust-Nera and Magadan–Ust-Om-chug–Kulu–Ayan–Uryakh–Tomtor–Agayakan. Routes were taken also along the Anadyr River from the Markovo village up to Yeropol and down to the Utyosiki; along the Mayn River, right-hand tributary of the Anadyr, up to the mouth of its tributary the Algan. The valleys of the Belaya River and one of its sources, the Bolshaya Osinovaya (from its upper reaches down to the mouth), were thoroughly studied, as well as the valley of the Amguema River in its middle and lower reaches and the valley of its tributary the Ekitiki. Material was also collected in areas adjacent to the southern coast of the Chaun Bay.

The landscape and habitat distribution of ants and the temperature conditions of their wintering were studied, as we have already mentioned, in the

upper reaches of the Kolyma (environs of the Aborigen Field Station) along an altitudinal zonal profile covering most of the habitats characteristic of the Kolyma Upland and of the Chersky mountain chain (the highest point is the Aborigen Peak, 2,286 m above sea level). The basic features of the landscape structure, climate and microclimate, soil cover, microflora, flora of lower and higher plants, vegetation and its production, and fauna and community structure of some invertebrate and vertebrate animal taxa were studied in this area; many works on the ecology of particular species and groups of plants and animals were carried out (Biologicheskaya stantsiya..., 1993).

The Kolyma Upland and the ranges of the Chersky mountain chain system differ both in true altitudes and in prevalent rocks: the upland is formed mainly of various slates, whereas the Bolshoy Annachag Range is formed mainly of granites. This difference has far-reaching consequences, showing mainly in the mechanical composition of the products of weathering: slates produce fine silty melkozem, which impedes drainage, whereas granites produce coarse gritty sand, which, on the contrary, facilitates the rapid outflow of water ("swallow" drainage). Drainage, in its turn, strongly influences the ice content of the permafrost, and consequently the seasonal thaw depth and, further, the type of soils, their hydrothermal regime, the vegetation and the invertebrate community.

In addition, the Bolshoy Annachag range, its branches and the depression of Jack London Lake display distinct marks of Pleistocene glaciations in the form of cirques, trough valleys, various moraines etc. The Alpine-type relief of the range contrasts with the smooth shapes of the slate-formed Kolyma Upland. The considerable altitude of the Bolshoy Annachag Range contributes to the diversity of landscapes and habitats it displays, greater than in any other part of the altitudinal zonal system of our region.

For determining the overwintering conditions of ants, nests of all the studied species were excavated both in summer and in winter, the depths of overwintering chambers and temperatures in the nests were measured in different species at localities with different substrate, humidity, exposure and true altitude. It is impossible to estimate temperature conditions of the wintering of ants (as well as of any other taxon of soil-dwelling invertebrates) based on information provided by the net of stations of the Hydrometeorological Service. In the 1970s and 1980s, only 17 of the 140 meteorological stations of the Magadan Region monitored the temperature of the soil at different depths with special thermometers; four other such stations worked in the upper reaches of the Indigirka; currently the total number of stations has decreased to 50, and the number of those that monitor soil temperatures to four (two of which are at the coast of the Sea of Okhotsk). However, the data provided by meteorological stations fail to represent the diversity of soil temperature conditions not only because of

the small number of observation sites, but also due to the peculiar positioning of the stations. The sites for constructing such stations should comply with certain standard requirements: above all, they should be removed to a particular (and quite considerable) distance from hills and forests, which influence the illuminance and the wind regime (Nastavleniya…, 1969). This is why meteorological stations usually stand on relatively dry, deeply thawing floodplain terraces with herbaceous vegetation, whereas most of the region is covered with mountain forest-tundras with moss and lichen vegetation and humid cold soils.

We wanted to estimate the temperature field not only in habitats prevalent in the study area, but also in habitats whose temperatures showed extreme differences from the zonal ones, because these are the habitats with species most exotic for the region. To achieve this objective, we measured the seasonal changes of temperature in ant nests and in the soil of different habitats in order to determine the lowest temperatures (most important for successful overwintering), the period when they are observed, the duration of the exposure of ants to these temperatures and to temperatures lower than 0, –5, –10, –15 and –20 °C, the lag of temperature changes in different soils, and other parameters of the thermal regime.

These results, in addition to their subordinate role, proved also self-sufficient, since they can be used for analysing the distribution of any organisms along the basic profile and in similar landscapes of the Upper Kolyma basin. Moreover, they provide characteristics of large areas of Siberia with continental climate covered in winter by the Siberian High (Alfimov, 2005)

The resistance of abundant ant species to low winter temperatures was studied by measuring the long-term tolerable temperatures ($LT_{50\%}$), the supercooling points (including their lowest values) and their seasonal changes in the overwintering stages typical of each species. The meaning of this approach is briefly explained below.

Ants belong to the group of cold-tolerant invertebrates capable of avoiding freezing by supercooling the fluids of their body (see Chapter 4). The lowest supercooling temperature is for such animals the lowest their organisation can briefly survive; freezing is inevitably fatal. The lowest supercooling temperature is easy to measure with a thermocouple, which records the release of heat caused by crystallization.

It was extremely important to determine for each local group of animals the value of its lowest supercooling temperature, because it implies, even if it is not statistically significant, that this value can be found in most individuals in populations of this species living under more severe conditions. Thus, the lowest supercooling temperature is an informative, objective and easy to measure parameter of cold-hardiness for species unable to survive freezing.

However, it is not always correct to use the lowest supercooling temperature as the only parameter of cold-hardiness. In many cases the mortality of invertebrates at constantly low temperatures depends on the period of exposure. It is, therefore, useful to determine the ratio of the temperature that kills half the individuals after long exposure (over 24 hours) and the average lowest supercooling temperature, and thus estimate whether the latter parameter is representative and sufficient. In view of this, we developed a special apparatus and determined the lowest negative temperature tolerable at long exposure in most of the studied species.

It should be emphasized that the ants used in cold-hardiness experiments were overwintering individuals from nests marked earlier (in autumn) in the immediate environs of the field station. Since the air temperature from December to February was virtually all the time considerably lower than in the nests, certain precautions were taken against cold shock. The soil monolith containing the nest was cut out of the ground and within half an hour brought into a cold room with temperature close to that of the overwintering chambers. The extracted individuals were immediately put into controlled-temperature containers with temperature the same as in the wintering chambers.

The transportation of species dwelling in habitats very remote from the station was much more problematic. Monoliths with the nests of *Leptothorax muscorum* were transported from the Oymyakon Depression (around 850 km away) in specially constructed controlled-temperature containers with a self-contained power supply, maintaining a temperature close to that of the wintering chambers. And some of the monoliths were safely brought to the station in the open body of an automobile at temperatures reaching as low as −30 °C.

The habitat with numerous colonies of *Formica candida* and *Myrmica bicolor* closest to the station is about 100 km away. Since the nests of these species cannot be extracted in monoliths from the pebble-sand ground of the floodplain, the nests were excavated and ants were extracted on site on days with air temperature not lower than −16 to −18 °C. The ants were then put into a portable controlled-temperature container or a vacuum flask with cryohydrate mixture of appropriate temperature, in which they were brought to the laboratory.

The final part of the study was the comparison of physiological capacities of ants to withstand sub-zero temperatures and the actual temperature conditions observed in different biotopes. This comparison helped us understand how insects unable to survive freezing withstand extremely severe winter conditions using an arsenal of diverse adaptations. The results of our detailed studies of the cold-hardiness of ants in other areas, such as the coast of the Sea of Okhotsk and southern and northern Finland (Berman & Zhigulskaya, 1995a, 1995b, 1995c), were also used in the book. These data helped us appreciate more thoroughly

to what extent the ability to withstand sub-zero temperatures determines the spatial distribution of ants, or, in other words, find out to what degree the spatial (biotopic and geographic) distribution of ants is limited by the relationship between physiological capacities and temperature conditions of wintering.

This part of the study is of special interest, because in many species of different invertebrate taxa the boundary of the geographic range runs through the mountain forest-tundras of the Kolyma Upland, and this is often reflected in their peculiar territorial distribution. Ants provide a useful model for such studies, for some ant species dwell here within a very narrow scope of habitats, whereas in others, on the contrary, this scope is considerably wider (compared to other studied regions of Siberia).

For preserving the integrity of the approach, we used only minimally the published and unpublished data on the biology of ants at the Upper Kolyma, mostly on rates of development, size and composition of families, fecundity, and other aspects of ontogeny observed during the active period in the life of ants (Kipyatkov et al., 1984; Zhigulskaya, 1987; Zhigulskaya & Tseytva, 1991; Zhigulskaya et al., 1992; Zhigulskaya & Kipyatkova, 1990). Work in these areas continues.

<p style="text-align:center">*   *   *</p>

Finally, probably in defiance of tradition, we, co-authors of this book, thank—each other. This book could never appear without the happy coincidence that brought us all (two zoologists, an ecophysiologist and a microclimatologist) together at the same time and at the same place, where we have stayed, in fruitful collaboration, over about 30 years.

PROFESSOR DANIIL BERMAN

CHAPTER 1
CLIMATE AND LANDSCAPES OF THE UPPER KOLYMA REGION

The ecosystem differentiation of the Upper Kolyma basin is not sufficiently known. Vegetation, which is often used as one of the main markers of this differentiation, in this area often fails to indicate the boundaries of ecosystems. The diversity of plant dominants among trees, shrubs, dwarf-shrubs, herbs and lichens is rather low in the region, and each of these dominants shows extremely high ecological valence in relation to both the hydrothermal regime (Figs. 2, 3) and soil conditions (Berman et al., 1990; Alfimov et al., 1994.). Therefore, in spite of the extreme diversity of the accumulated positive temperatures of this area (see below), which differ by a factor of 3.6 at a depth of 5 cm and by a factor of 400 at a depth of 20 cm (Berman & Alfimov, 1992), the diversity of ecosystems is relatively limited.

The tree species especially responsible for this situation are the larch *Larix gmelini* and the Siberian dwarf pine *Pinus pumila* (Figs. 2, 3). Both species have huge ranges and absolutely dominate the mountain forest part of the area, covering the slopes of any exposure and other elements of the relief with entirely different permafrost conditions (with seasonally thawed layer—STL—from 0.3–0.4 m to 2.5–3.0 m) on soils of every kind (Photos 1, 2, 3). The habitat distribution in the larch is limited, above all, by the severe wind regime of the winter, and in the dwarf pine, also by waterlogged ground. Naturally, the proportion of mountain areas with such conditions is small. The position of the upper altitudinal boundary for the larch and the dwarf pine is determined, in addition to the wind regime in winter, by the lack of heat in summer (Berman et al., 1990).

Both species produce acidic litter contributing to the depletion of the soil cover (and of the entire biota) and its "levelling" over vast areas. The larch, due to the incomplete development of the canopy, is a weak determinant species in sparse forests and, the more so, in thinned tree stands; it determines rather the structure of the vegetation than its floristic composition (Demyanov, 1980). The Siberian dwarf pine, on the contrary, is a potent determinant, largely because of
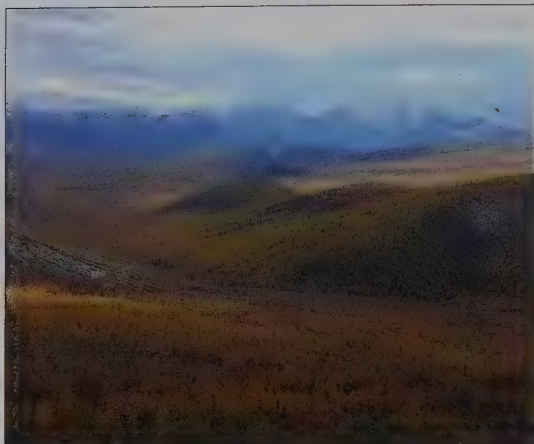
Photo 1. Dominance of the larch in the mountain forest belt, except in its upper part, is especially visible in autumn, when the landscape is coloured in brownish yellow. Meanwhile, Siberian dwarf pine is present everywhere in the undergrowth, but at this time of year it is hard to spot.
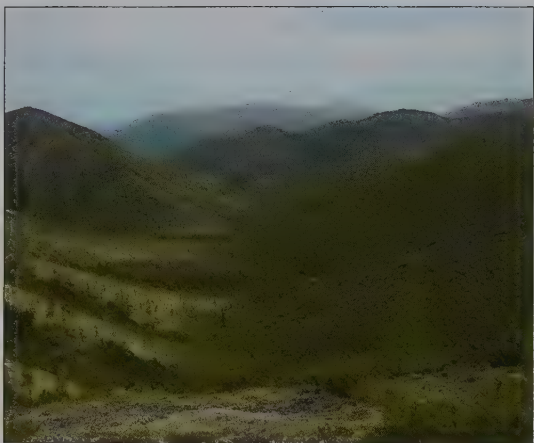
Photo 2. Valley oriented strictly from east to west, altitude around 1000 m, therefore contrast between north- and south-facing slopes very clearly pronounced: south-facing slopes are covered by continuous tangles of pure Siberian dwarf pine; north-facing slopes, by lichen communities with thinned stand of larch in convex parts and by moss communities with larch and alder in erosional depressions. However, both on northern and on south-facing slopes at such altitude hypoarctic ants can be found, on south-facing slopes sometimes accompanied by *F. exsecta*.

Photo 3. In the upper part of the belt Siberian dwarf pine is clearly dominant, since, unlike the larch, it is capable of lodging at low temperatures, and if covered with snow does not suffer under strong winds from snow corrasion and frostbites.
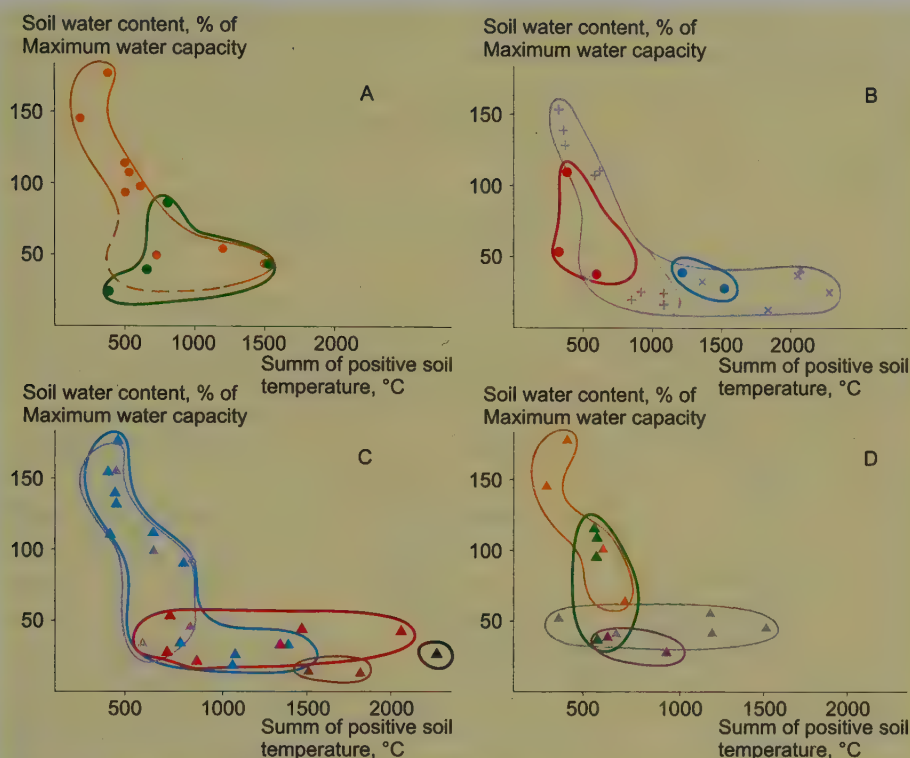
Fig. 2. Hydrothermal conditions in the soil layer at the depth of 0–20 cm in stands with different tree species and under surface cover of different types in the Upper Kolyma basin. Ordinate, soil moisture content, % of the maximum moisture capacity (MMC); abscissa, annual sum of positive average daily temperatures. Localities where hydrothermal parameters were measured and approximate boundaries: (A) larch, orange circles and line; Siberian dwarf pine, green circles and line; (B) alder, red circles and line; aspen, blue circles and line; area without trees, violet circles and line (oblique dagger, sparse larch forest zone; straight dagger, mountain tundras); approximate boundary between mountain tundras and areas without trees in the sparse larch forest belt, dash-dot line; (C) mesophile heather dwarf-shrubs (except cowberry), violet triangles and line; cowberry, red triangles and line; lichens, blue triangles and line; sedges, brown triangles and line; steppe herbs, black triangles and line; (D) reedgrass, *Calamagrostis*, lilac triangles and; green mosses, green triangles and line; sphagnum, orange triangles and line; dead-cover communities, gray triangles and line.

the thick shade it provides, thus strongly decreasing the heating of the surface, already scant even without the shade. Decreased heating leads to the depletion of the surface cover and to the dominance of widespread species of lichens, mosses and dwarf-shrubs. This is why the larch and the dwarf pine, as a rule, reflect
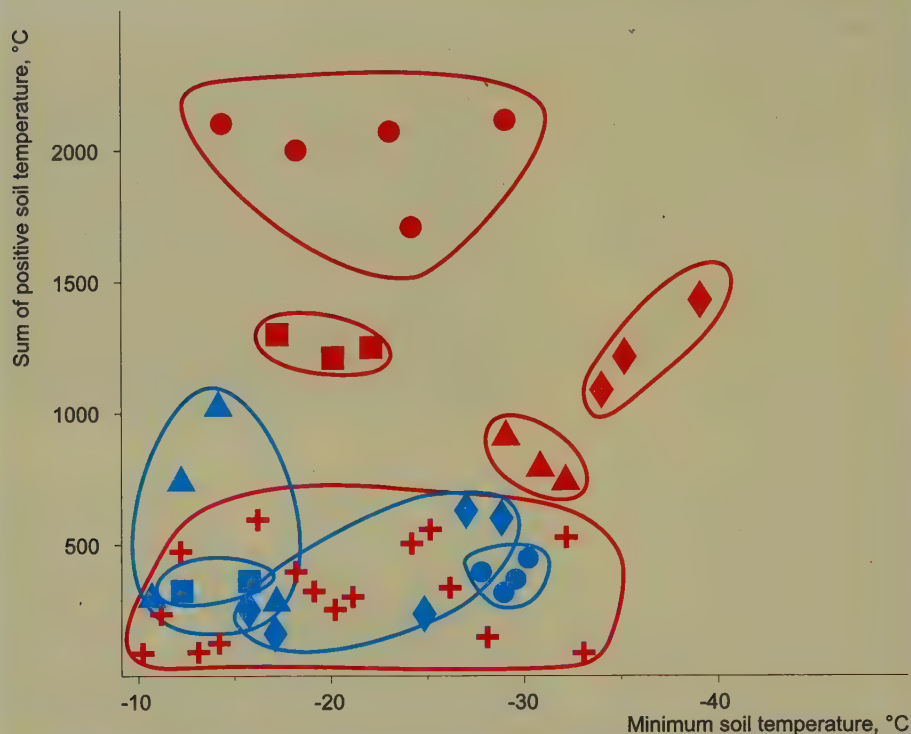
Fig. 3. Distribution of principal ecosystems in the field of winter and summer temperature parameters of the upper cm of soil. Red marks and lines: relict steppes on south-facing slopes, circles; sedge communities on ridges and edges of terraces, diamonds; larch, aspen and birch forests on dry south-facing slopes, squares; lichen-moss mountain tundra on plateau-like surfaces, triangles; various forest ecosystems on terraces, north-facing slopes and floodplains with dominant Siberian dwarf pine, willows, poplars or larch, crosses. Blue marks, and lines: moss-lichen larch forests on trains of slopes, squares; herb alder and birch forests in concave areas of south-facing slopes, diamonds; lichen-dwarf shrubs mountain tundra on south-facing slopes, triangles; lichen-moss tundra on north-facings slopes, circles.

neither the spatial structure of the aboveground vegetation, nor the differences of the invertebrate communities. Unfortunately, the ecological valence of most other dominant plant species is not sufficiently known, and it appears impossible to consider ecosystem and landscape differentiation based on these species.

The landscapes of the Upper Kolyma basin were most thoroughly described by G. N. Egorova (1980, 1984, 1986) based on the concept developed by N. A. Solntsev (1973, 1977). According to this concept, landscape formation is based

on the so-called morpholithocomlexes, influenced by factors of lower order, such as altitude, exposure, climate, permafrost etc. We used the larger divisions of the territory according to Solntsev and begin this chapter with a brief description of the above-mentioned factors.

FACTORS OF LANDSCAPE FORMATION

Relief and altitudinal belts. Most studies of the ecology of ants were carried out in the basin of the Sibit-Tyellakh, a small left-hand first-order tributary of the Kolyma (length around 20 km), and in the depression of Jack London Lake, adjacent to the upper reaches of this river. The approximate coordinates of this area's centre are 62° N and 149°30' E (see Fig. 1). The upper part of the Sibit-Tyellakh basin occupies the eastern macroslope of the Bolshoy Annachag Range, part of the Chersky mountain chain system. The axial part of the range is granite batholith embedded in the sandstone-slate formation typical of the entire Okhotsk-Kolyma Upland (Shilo, 1970). The range is crowned with a number of peaks with altitudes over 2000 m above sea level (Vlastny, Shishak, Stremleniya, Aborigen). The relief of the upper part of the Sibit-Tyellakh basin, situated within the area of granite distribution, has pronounced alpine aspect, with clear marks of several Pleistocene glaciations in the form of troughs, cirques, hanging valleys and rock-bars at different altitudes. The interfluve of the Sibit-Tyellakh and the Kolyma, as well as the branches of the Bolshoy Annachag Range along the right bank of Sibit-Tyellakh, are formed mainly of slates and represent typical medium mountains with altitudes up to 800–1000 m above sea level, and with smoothed relief. Part of this altitudinal interval is occupied by moraines of different ages forming vast landscape units with numerous lakes. Near the mouth of the Sibit-Tyellakh, the terraces of the Kolyma valley are clearly pronounced. The character and diversity of conditions of this entire area are quite representative of the Kolyma Upland, whereas the Bolshoy Annachag Range is likewise representative of the Chersky mountain chains.

Several altitudinal belts, typical of the hypoarctic type of altitudinal zonation, are distinct in the upper Kolyma basin, in spite of the severe climate and the relatively small range of altitudes (Ogureeva, 1998, 2000). The mountain forest (or mountain taiga), mountain tundra and golets (or alpine rock) belts are usually recognized. The vegetation of these belts in the basin of the Sibit-Tyellakh was described in detail by V. B. Dokuchaeva (1980, 1985). The mountain forest belt occupies the area from the bank of the Kolyma to 800–1000 m above sea level. Altitudes between 800 and 1200 m are occupied by a peculiar zone of transition from sparse forests to mountain tundras, in the form of a mosaic of

thinned larch stands and Siberian dwarf pine and mountain tundra communities. Above 1200 m is the mountain tundra belt.

Permafrost conditions. The study area, like the entire Northeast of Asia (with the exception of the Sea of Okhotsk coast), is completely covered by permafrost, since the average annual air temperatures in this area are from −9 to −11 °C. The temperature of the permafrost at depths of 11–15 m, where it remains unchanged throughout the year, is −4 to −5 °C. The thickness of the layer that thaws during the warm season (STL) varies from 0.3 to 3.5 m (Kalabin, 1960; Nekrasov & Mikova, 1975; Germanov & Klimovsky, 1976; Alfimov, 1984, 1985). As in any mountain area, the pattern of the changes of STL, which controls ecosystem processes, is complicated, because it depends on many factors determining the heat exchange at the surface and the thermophysical properties of the soil (Gorbunov, 1970, 1976; Romanovsky & Lisitsyna, 1984; etc.). The parent rock (or, to be more precise, the type of its weathering products, which determines the character of drainage), the position in the landscape (altitude, degree of exposure), the thickness of the organogenic horizon of the soil, the density and type of vegetation (especially mosses and lichens) are among the most important of these factors.

In the study area, the depth of STL depends mostly on the type of the parent rock. At altitudes lower than 800–1000 m above sea level, parent rocks are mostly clay-slates, the weathering of which produces fine particles. The drainage of such grounds is impeded, and they are saturated with water, which eventually leads to the formation of ice-bearing permafrost; its seasonal thawing requires much heat. STL in such areas is especially thin (no more than 30–40 cm) in biotopes with moss-lichen cover, where the thawing sometimes fails to reach the mineral horizons and is restricted to the organogenic ones: peat and peat-rich. However, on the steep south-facing slopes with very rubbly ground drainage is always of the "swallow" type, even if the parent rock is slate. The soil and the ground of such slopes is strongly warmed and dried, the surface cover is thinned, and the depth of STL is sometimes greater than 2.5–3 m. Even below this, frozen water exists only in the form of separate, not interconnected crystals. This is the so-called dry permafrost.

In the mountain tundras of the Bolshoy Annagach Range above 800–1000 m granites are prevalent, and the products of their weathering are coarse-grained and almost invariably provide swallow-type drainage. Therefore, in spite of the shorter and colder summer of the top altitudinal belt, the thickness of the thawed ground here already reaches 40–70 cm by June. For comparison, in sparse forest ecosystems with ice-bearing permafrost, where thawing starts 15–20 days earlier, at this point it reaches only the depth of 15–20 cm. Even

the coldest areas of the mountain tundra, north-facing slopes covered with thick snow, thawing reaches by the beginning of August deeper than 120 cm. It should be emphasized that such considerable thawing of the soil and the ground is not a distinguishing feature of mountain tundra landscapes; it is due entirely to the type of the soil-forming rocks. In adjacent mountain ranges formed of slates the depth of thawing at the same altitudes as those of the Bolshoy Anna-chag mountain tundras usually varies by the end of the season between 40 and 70 cm, reaching more than 120 cm only under special conditions (on ridges, at slope bends and on south-facing slopes under thinned surface cover).

The thickness of STL varies considerably within the same altitudinal belt and on the same types of rock, depending on the combination of the mentioned factors. Other conditions being equal, the deepest thawing takes place on rubbly talus slopes (sometimes as deep as 90 cm even on slopes of northern exposure). The presence of lichens, mosses or dwarf-shrubs decreases the amount of heat reaching the soil, and the depth of STL decreases to 60–70 cm. It decreases fur-ther with further development of the surface cover, increase of the foliage pro-jective cover and accumulation of peat and melkozem in the soil. In lower parts of slopes and in small depressions it sometimes drops as low as 20–25 cm and, as we have mentioned above, thawing sometimes fails to reach mineral horizons.

The variation of STL thickness is greatest on slopes of southern exposure with highest intake of solar energy and highest diversity of soils and vegetation. In humid closed birch and alder forests on transitional parts of the slopes with dense herbaceous or moss–dwarf-shrub cover and turf or peaty and rubbly soils STL is no thicker than 70–90 cm, and on mossy peaty ground (lower parts) of slopes its thickness decreases to 35–40 cm. On fire sites with skeletal soils and on relict steppe areas with non-closed xeromorphic cover, STL, on the contrary, reaches a depth of 60–80 cm within 7–10 days after the snow melts, and by the end of autumn sub-zero temperatures are observed, as we have noted above, only at depths of 2.5–3.0 m.

The range of STL depth on terraces of different origin is almost the same as on south-facing slopes: from 0.4 to 2.0 m. The key factors, as in other areas, are the drainage conditions and the type of vegetation. In shallow depressions with sphagnum in larch forests the depth of STL is the same as on stagnant wetlands (45–50 cm), and in both cases 25–35 cm of this layer is peat and unconsolidated sphagnum, whereas the thawed mineral horizon is only 5–10 cm deep. Rubbly plateaus with thinned surface cover and with primitive soils or sandy levees with larch forests thaw deeper than 1.5 m.

The only parts of the study area without permafrost are in the floodplains of large rivers. The so-called talik zones are sometimes formed in such flood-plains, warmed by the proximity of the riverbed and thus usually ribbon-shaped.

However, the upper horizons of soils and the ground in most of the floodplain in winter freeze (partly due to the winter low water) as deep as in areas outside the floodplain with the same soil water content and thickness of snow.

It will be shown below that the cooling and humidifying effect of the permafrost on the upper 5–10 cm of the soil is present during the entire warm season only if the surface of permafrost lies no deeper than 40 cm. Landscape units with such STL depth occupy only a small part of the area of the Upper Kolyma basin.

Climate. The basin of the Upper Kolyma is an area with subarctic climate, with very cold and dry arctic air dominant in winter and the air masses of the temperate zone dominant in summer. The character of the climate is determined by the position of this area between two regions with dramatically different air masses over the whole year: the extreme continental northeastern Yakutia and the northern coast of the Sea of Okhotsk with its cold maritime climate, termed monsoon by some authors (Alisov & Poltaraus, 1966). In winter the Upper Kolyma basin is at the southeastern periphery of the Yakutia branch of the Siberian High; in summer the air pressure pattern is more blurred, and the climatic front dividing the air masses of continental and marine origin runs somewhat to the west of the area. The transitional character of the climate makes it difficult to identify its type with certainty, and its mixture of features typical to both continental and maritime regions makes it unique. N. K. Klyukin (1960) called it the climate of "tundra and forest-tundra within forest". In winter, along with pronounced continentality, this area has relatively thick snow cover (on the average, 40–50 cm) and in some places this is extremely uneven. Air temperatures sometimes drop almost as low as at the same altitude in northeastern Yakutia (the average January temperature at the nearest weather stations is around −34 to −36 °C, and the average absolute minimum is −53 to −55 °C). Higher wind speeds often make the weather even more severe than at the "Pole of Cold". The summer is relatively warm: the average July temperature is 13–14 °C and the sum of above-zero temperatures over the warm season is around 1300 °C. Total annual precipitation is 300–450 mm, most of it falling at the second half of summer due to the intrusions, common at this time of year, of cyclones from the Sea of Okhotsk, which bring continuous, but not abundant rains. The ratio of possible evaporation and precipitation (Budyko, 1971) varies from 1.5 to 0.5 and decreases with altitude (Klyukin, 1960), so that humidification is moderate at lower altitudes and abundant at higher altitudes.

One of the most important consequences of the annual change of air masses from continental to oceanic, quite different in their temperatures and in the content of water, is the considerable long-term fluctuation of climatic param-

eters (Photos 4, 5). The number of considerable (over 10 °C) deviations from the normal average monthly temperature both in the cold and in the warm season in the Upper Kolyma basin is unmatched not only in the subarctic zone, but in the entire territory of Russia; in winter these deviations are sometimes as great as 18–20° C (Gedeonov, 1967).

All that was said above about climate refers to the intermountain depressions lying between altitudes of 300 and 800 m above sea level and covered mostly with sparse larch forests. At higher altitudes summer air temperatures decrease, and total precipitation, proportion of solid and mixed precipitation, wind speed (especially in winter) and number of cloudy days increase. Summer becomes colder and shorter, and the duration of winter increases from 220 days in the valley to 245 days at an altitude of 1250 m above sea level (Alisov, 1956).

The most typical feature of the climate of the Upper Kolyma basin, as well as of most of the continental Northeast of Asia, is the inverted distribution of winter temperatures. The dominance of the anticyclonic, largely cloudless weather leads to the strong radiation cooling of the lower strata of the atmosphere. The coldest and, thus, the densest strata tend to be at the surface of the earth, leading to the formation of stable stratification, which, in its turn, contributes to further development of radiational cooling and temperature decrease in the lower strata. In mountain relief this process is enhanced by the flow of cold air from higher areas to the bottoms of valleys and depressions. It is this combined effect of radiational cooling and cold air downflow that leads to the formation of the lowest winter air temperatures of the Northern Hemisphere in the mountain depressions of northeastern Yakutia. Reaching their extreme at the bottoms of valleys and depressions, lowest temperatures already start increasing on the lower parts of mountain slopes with a gradient reaching 5.4 °C per 100 m altitude, and this may sometimes lead to a difference of 19° between the altitudes 500 and 850 m above sea level (Alfimov, 1984). At higher altitudes the rate of temperature change decreases, inversions are more often disrupted by the intrusion of cyclones, and the total difference between average lowest temperatures in mountain tundras and sparse forests is 15–20°C (–37 to –40 °C and –53 to –55 °C, respectively).

The difference between altitudinal belts in precipitation is also considerable: 300–400 mm in sparse forests and 500–600 in mountain tundras. The wind regime is also different, especially in winter: in the valleys winds are observed only during the periods when inversion is disrupted (i.e. after the intrusion of deep cyclones), whereas on mountain tundras they blow virtually all the time. Accordingly, the number of days with snowstorms is 11–26 in the valleys and almost 10 times greater on the tundras: 100. The resulting difference between climatic parameters of the belts is quite considerable: the climate of the valleys

Photo 4. Snow in the Kolyma Upland in July. In a few days all the larch forests changed their colour to the typical autumn brownish yellow.

Photo 5. Late spring, 2003. Abundant snowfall on May 22 slowed down all phenological processes.

of the Upper Kolyma is comparable with that of the depressions of northeastern Yakutia, recognized as the Pole of Cold and continentality of the Northern Hemisphere, whereas the key parameters of the climate of mountain tundras are similar to those of the zonal tundras of Chukotka (Alfimov & Bulgakov, 1980).

Factors of microclimate formation. The action of altitude, permafrost, exposure, drainage and soil water content, nanorelief, type of vegetation—especially surface cover—create considerable variation in the microclimate of the soil, showing especially clearly in the seasonal fluctuations of temperature of the soil's upper layers. Differences in the sum of above-zero temperatures over the warm season, an integral parameter of soil temperature regime largely determining the living conditions of soil animals, reach a factor of 3–4 at the surface and a factor of 100 at the depth 20 cm. The formation pattern of the summer temperature regime was treated in detail in our earlier works (Alfimov, 1984, 1985) and we are not discussing it here. The key factors of microclimate differentiation in the landscapes of the Upper Kolyma are outlined below.

The thermal regime of the surface of even the most ice-saturated and weakly thawing areas of the sparse forest belt depends on altitude, exposure and type of vegetation, whereas the heating of soil horizons lying deeper than 5 cm is influenced, above all, by the type of permafrost (ice-bearing or dry), which, in its turn, is determined by the type of soil drainage. The temperatures within the soil with ice-bearing permafrost deeper than 5 cm, almost independently of other factors, are more or less equally low. Similarly, the hydrothermal regime of all the deeply thawing (dry permafrost) biotopes is similar, with only one reservation that the heating conditions not only at the surface, but also in the deeper layers depend mostly on the traditional parameters (altitude, exposure, type of vegetation etc.). As for the ice content of permafrost, its distribution in the mountain relief and the thickness of the seasonally thawed layer, these parameters are, as described above, determined by the geology and geomorphology of the locality, heat exchange conditions at the surface and thermophysical properties of the soil.

Nanorelief plays an extremely important part in the life of ants, especially in water-saturated biotopes with little shade. Tussocks and hollows differ not only in degree of soil water content, but in the ways solar energy is consumed: on tussocks it is mostly heating and in hollows mostly evaporation. Differences in temperature parameters between adjacent elements of nanorelief (tussock and hollow) on peaty trains of south-facing slopes are quite comparable with those between dry south-facing slopes and bogs.

The duration of the warm period in the soil is an important parameter of the heating conditions of biotopes. The warm period of the coldest areas in

the soil of south-facing slopes at a depth of 20 cm is three weeks (or 15–20%) shorter than that of the warmest areas on the same slopes. In mountain tundras this parameter is 1–1.5 months shorter, and its brevity, in spite of the similar values of highest temperatures, considerably influences the heating conditions. The greatest differences in the duration of the warm period, reaching 2 months, are observed in the study area between relict steppe slopes in the valleys and lichen-moss northern slopes in the mountain tundra.

ECOSYSTEMS OF THE AREA

All that has been said above shows that the pattern of landscapes in the study area is rather varied. The heating conditions of the warmest parts of the valleys (relict steppe areas) are comparable with those of the mountain steppes of South Siberia, whereas the lichen communities of mountain tundras are similar to the typical tundras of Chukotka (Krasnoarmeysky Meteorological Station) and Taymyr (Ust-Tareya Meteorological Station) (Alfimov, 1984). Thus, the maximum differences in the microclimate in only two adjacent altitudinal belts, mountain forests and mountain tundra, are as great as the differences between the typical at the ends of a series of six geographcal zones and subzones (steppe, forest-steppe, mixed and broad-leaved forests, taiga and tundra).

The border between the sparse forest belt and the mountain tundra belt, which occupy approximately equal areas, is a border of the greatest importance. As fundamentally important, although less pronounced, is the border of the talik zones in river floodplains, which are, as we have already mentioned, dramatically different from the rest of the floodplains in hydrothermal conditions of the deeper layers of the ground, and in the type and functioning of the ecosystems.

Ecosystems of the sparse larch forest belt. This part of the area is formed mostly of various slates, sandstones, aleurites and aleurolites; carbonate rocks are rare in this zone. The shapes of the relief are mostly smooth; only at the periphery of the high-mountain massifs there are areas of glacial accumulation. The landscape of this zone is dominated by sparse forests and thinned tree stands of the larch, with the Siberian dwarf pine covering the convex, well-drained elements of the relief. The background landscape is interspersed with small areas of alder (*Alnus fruticosa*), aspen (*Populus tremula*) and birch (*Betula platyphilla*) forests, various meadows, including xerophile, and relict steppes. Some authors (Parmuzin, 1979) recognize a separate belt of Siberian dwarf pine at the border between sparse larch forests and mountain tundras, while others (Pivnik, 1958; Yurtsev, 1964) believe that the dwarf pine here, as well as in other areas of the

Northeast of Asia, forms no separate altitudinal belt. Indeed, the dwarf pine is not dominant in the mountains everywhere, but only in areas with favourable edaphic conditions. On the other hand, it occurs more or less regularly through-out the altitudinal interval of the sparse forest belt, usually together with the larch, forming thick tangles virtually in every well-drained area. In other words, the dominance of the dwarf pine in upper areas of the mountains is probably not determined by climate (Fig. 3).

Ecosystems of slopes. Flat and concave parts of slopes with northern exposure are mostly covered by thinned boggy larch stands with a very high position of the surface of permafrost (at a depth of 30–60 cm), sharply contrasting in microclimate with the convex elements of the microrelief. Their most important feature is the considerable amount of water flowing in the layer 5–10 cm above the surface of permafrost, dozens of times greater than the amount of precipitation (Alfimov, 1989; Berman et al., 1990). Hillocks receive less water than low spots between them; as a result, the cover includes more sphagnum at the low spots and more dwarf-shrubs, lichens and green mosses on the hillocks (Photos 6, 7, 8).

In spite of the proximity of permafrost to the surface, constantly low temperature (the annual sum of above-zero average daily temperatures of the soil is 1000 °C at the surface and 50° at a depth of 20 cm: Berman & Alfimov, 1992) and water saturation, soil invertebrates are quite abundant in these areas, mostly due to enchytraeid worms (over 1000 individuals per square metre[1]), concentrated at the lower boundary of the peat horizon, and lithobiid centipedes (150–200) and diplurans (90–110), dwelling in the soft mass of the peat. Beetles, as in other "cold" habitats, are not numerous, but they are represented by typical northern species: the ground beetle *Pterostichus agonus* and the click beetles *Sericus brunneus* and *Denticolis varians*, with the latter switching from dendrophily to soil-dwelling. Some insect species penetrate through northern slopes from mountain tundras above (the grasshopper *Primnoa polaris*, the ground beetle *Carabus kolymensis*), occurring nowhere else in the sparse forest belt.

In the narrow gullies, alder forests are rather common, usually not mixed with any other tree species, in most cases with dead cover or with Labrador Tea (*Ledum decumbens*) and sphagnum. The composition of the invertebrate community of such places differs considerably from the background in the abundance of virtually every group, probably due to the dense canopy, which decreases insolation (Photo 9). For instance, the abundance of enchytraeids decreases to 100 individuals per square metre, the abundance of lithobiids to 60, all the species of ants, grasshoppers and click beetles completely disappear (although click

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[1] Hereinafter, according to results of Tullgren funnel extraction.

Photo 6. Flat and slightly concave parts of northern slopes are always covered with "hanging" bogs. Grounds are thawing poorly (to 30–60 cm), due to lack of heat, water is oozing, and colonizing mosses contribute to poor thawing. On steeper areas ground slips down in large blocks on permafrost table (solifluction), forming "drunken" forests. Here, like in areas with dominant lichens (Photo 7), hypoarcitc ants are common, but their abundance is low.
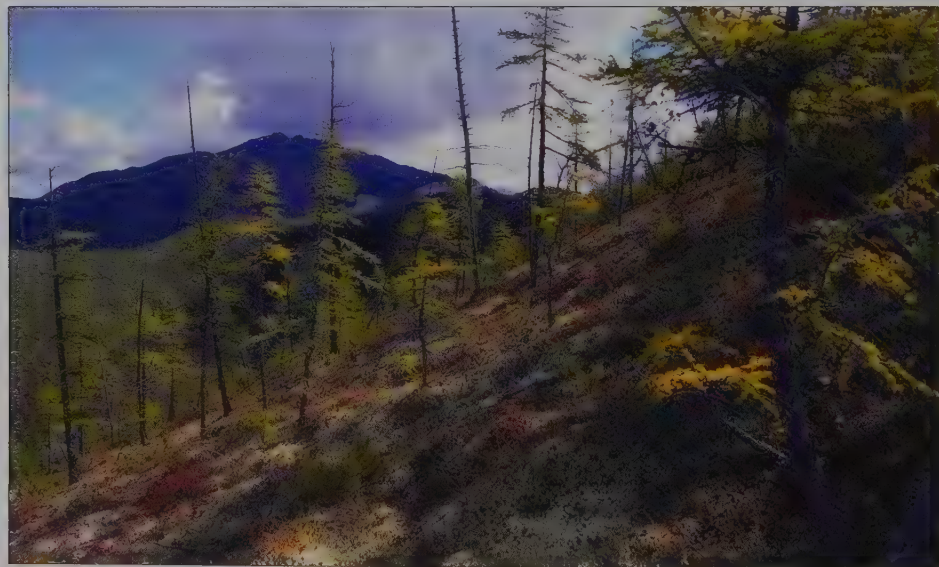
Photo 7. Less steep part of the same slope. Solifluction barely developed; lichens are dominant.

Photo 8a, b. "Drunken" forest in winter (a) and summer (b).

Photo 9. Thalwegs of deep erosional depressions on slopes facing any direction are often covered with alder (*Alnus fruticosa*), its closed canopy producing very deep shade. Either sphagnum or Labrador tea cover is usually formed in such areas; communities with dead cover are also quite common. These are the coldest biotopes, never inhabited by ants.

beetles occur in clumps of moss). On the other hand, the small ground beetle *Notiophilus fasciatus*, found nowhere else, is very abundant here, as well as the larvae of tipulids (over 100 per square metre), virtually absent in the larch forests described above.

The convex areas (*uvaly*) of the north-facing slopes are invariably occupied by Siberian dwarf pine communities, usually of the dwarf-shrub–lichen type with deeper position of permafrost.

The ecosystems of the south-facing slopes also segregate depending on the relief. Flat and convex areas are occupied by sparse larch forests with Siberian dwarf pine, alder, dwarf-shrubs and lichens (Photo 10, 11, 12). In areas without solifluction relief and in convex parts of solifluction terraces a uniform cover of sparse cowberry (*Vaccinium vitis-idaea*), several species of lichens and, sporadically, dog rose is formed. In concave parts of the terraces, due to high soil water content, green mosses, Labrador Tea and Middendorf's birch (*Betula midden-dorffi*) dominate, sometimes under the canopy of alder clumps. Concave areas of
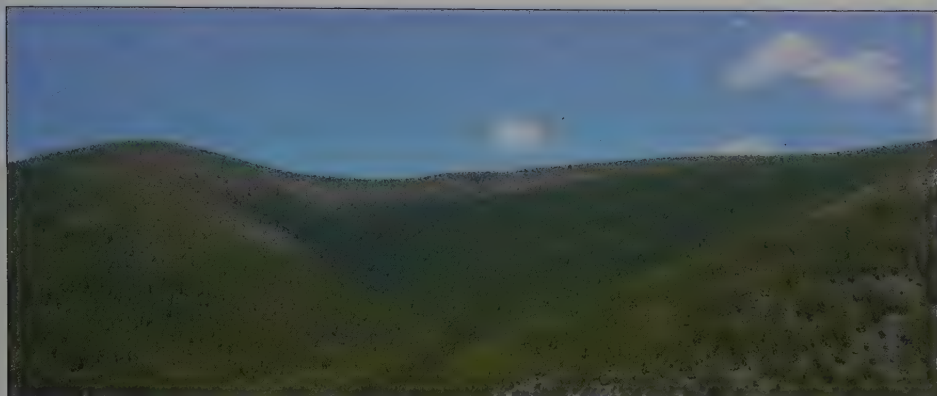
Photo 10. Larch forests covering south-facing slopes sharply differ from those covering north-facing slopes and their trains. Because of better heating, depth of seasonally thawed layer varies in different areas from 1.5 to 2.5–3 m even on slopes with deluvial mantle, and permafrost has no effect on root-inhabited horizons. Straight parts of slopes and negative forms of relief are covered with regular, not sparse forests. Mesoxerophile species, *F. lemani* and *M. angulinodis*, often occur here together with hypoarctic ants.
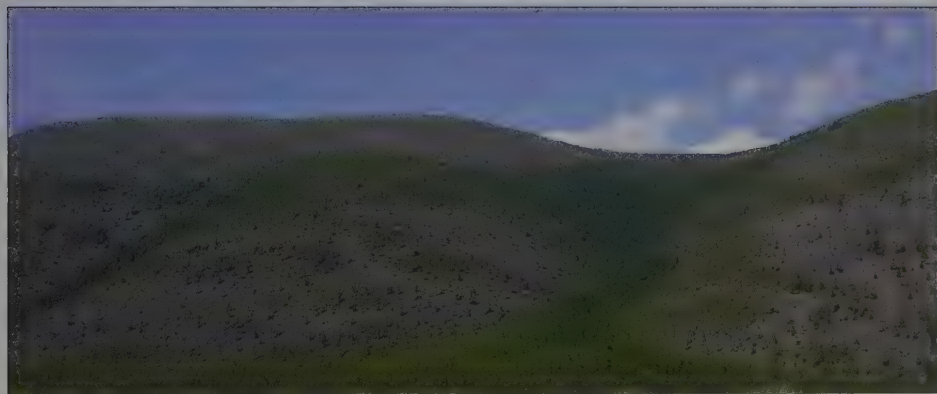
Photo 11. On convex south-facing slopes sparse dwarf-shrub–herb larch forests with Siberian dwarf pine of various degree of canopy closure are common. *F. lemani* is dominant here, while hypoarctic species are forced under larches and dwarf pines.

the south-facing slopes are occupied, depending on their relief, by alder forests with dead cover (in narrow gullies) or by closed larch or birch dwarf-shrub–green-moss forests (in wide erosional depressions).

The invertebrate community of the south-facing slopes is also, like the vegetation, distinctly different not only on convex and concave slopes, but also on elements of solifluction relief. For instance, the communities of sparse larch forests on south-facing slopes have little in common with those of the north-

Photo 12. Larch in a sparse forest. *F. gagatoides* dwells in the shadow of its canopy; the clearing behind the tree is inhabited by *F. lemani*.

ern slopes described above. In weakly shaded areas and cleanings chilopods are relatively few (around 50 individuals of both Lithobiidae and Geophilidae per square metre), and the taxa prevalent in abundance are ants (see Chapter 2), diplurans (over 300), spiders (around 200), coccids (over 200) and beetles of different families, the most abundant being Staphylinidae and Cantharidae (60–70 each). The invertebrate community of the concave areas of solifluction terraces, especially if mosses and Labrador Tea are prevalent in the cover, is fundamentally different and closer to that of the northern slopes than to that of the adjacent habitats.

The narrow (usually not wider than 50 m) bands of alder forests occupying deep depressions are also, like the alder forests of the north-facing slopes, in sharp contrast with the background vegetation. The alder forests formed in depressions of the south-facing slopes mostly have dead surface cover and less often herbaceous cover, with thawing to the depth of 80–100 cm, i.e. the same as in the alder forests of the north-facing slopes. The invertebrate community in the dead-cover alder forests of narrow depressions is similar to that of the alder forests of the north-facing slopes: they are also dominated by enchytraeids (over 500 individuals per square metre) and tipuloid larvae (124); myriapods are relatively rare (no more than 10), and ants are absent. It should be noted that the alder forests of the study area do not reflect exposure: they are always confined

to depressions and other elements of the relief with flowing water, sometimes only in spring and summer. Individual clumps of alder occur in different ecosystems up to the lower boundary of mountain tundras, and they are also always confined to areas with high and usually not constant humidification. The surface cover and the invertebrate community under large individual clumps, as well as in closed tree stands, differ dramatically from those of the background, due to the strong determinant capacity of the alder forest.

The ecosystems of the slopes with eastern and western exposure, varying in relief, steepness and parent rocks, are generally more similar to the ecosystems of the south-facing slopes than to those of the north-facing slopes. Most of the area on the eastern and western slopes is never occupied by mesohygrophile communities, but divided between mesoxerophile ones, similar to those of the south-facing slopes.

The ecosystems of deluvial trains—superficial deposits of various kinds, which make up the gentle lower slopes of mountains in regions with permafrost activity, differ considerably from the background ecosystems of the slopes (Photos 13, 14). Mildly sloping trains resting on terraces are usually waterlogged and have dwarf-shrub–green-moss, green-moss–lichen or sphagnum cover and ice-bearing permafrost close to the surface. The invertebrate community of these trains varies depending on their position, but is, in general, typical of peaty soils, with abundant chilopods, spiders, small fly larvae, and beetles (except Staphylinidae).

Another widely distributed type of slope train is the one with characteristic fan-shaped microrelief, comprising gully-like depressions separated by more elevated areas (Timofeev & Vtyurina, 1978) with contrasting distribution of all the components of the ecosystem. Trees are mostly confined to the elevated areas, between the gullies, occupied with dwarf-shrub–lichen communities, often with dominant cowberry, if the drainage is good, and with dwarf-shrub–green-moss communities if the drainage is somewhat poorer. In the depressions themselves, either sphagnum and Labrador Tea (Photo 15), or *Polytrichum* mosses are prevalent. Sharply contrasting temperature conditions, humidity, vegetation and invertebrate communities sometimes form here even in localities separated by the distance of one metre. The contrasting character of the beetle community in elements of gully relief is demonstrated by Table 1.

In spite of some slight variation in steepness, exposure-related difference in the heating of the soil surface of the slope trains remains the same. However, due to the strong insulating effect of the moss cover, these differences influence the temperature regime of only the upper 4–6 cm. The thermal conditions of deeper layers (e.g. in the peaty soils of the trains of south-facing slopes) differ little from those of the soils of north-facing slopes.
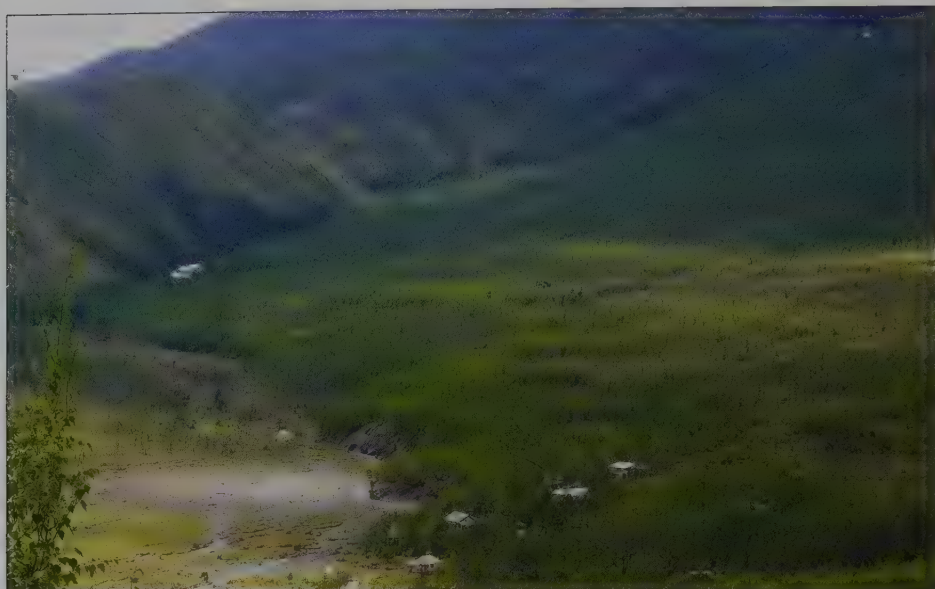
Photo 13. Moss-lichen sparse larch forest with ice-bearing permafrost on the train of a gentle slope, a typical element of Kolyma landscapes. It is the realm of the hypoarctic ant complex (*C. herculeanus, F. gagatoides, L. acervorum*), which is accompanied by *M. kamtschatica*.

Photo 14. Area of such a train covered with old sparse forest. Dense surface cover impedes colonization by ants; nests of all species are not numerous.

Photo 15. The same part of the train, but in an erosional depression with continuous sphagnum cover. Border between "tow" of moss and already formed peat is clearly visible.

Table 1. Abundance of beetles (individuals per m²) in different microrelief elements in a moss-lichen sparse larch forest on the train of a southern slope

Taxon	Higher area between gullies	Gully
All beetles, including	736	146
Elateridae	668	2
Cantharidae (larvae)	26	60
Staphylinidae	18	78
Other families	24	6

The ecosystems of alluvial cones of relatively small erosional depressions are often clearly pronounced against the background described above. The convexity of these cones leads to improved drainage and to the formation of sparse larch forests with Siberian dwarf pine or pure tangles of the latter. The upper parts of the trains of the south-facing slopes also stand out distinctly against the background vegetation. They are marked by rather narrow bands (from a few metres to several dozen metres wide) with relatively rich vegetation (compared to the slope and the train), including alder, birch, and larch with herbaceous

cover. These communities exist here because the depth of groundwater in these bands is optimal for vegetation (greater than in the wet train, but less than in the dry slope). This depth, in its turn, is determined by the depth of the surface of the ice-bearing permafrost. These bands are also distinguished from both the slope and from the rest of the area by the accumulation of considerable amounts of snow in winter, which improves the temperature regime of the soil.

The ecosystems described above occupy mountain slopes and trains. The pattern of the spatial distribution of ecosystems on accumulative forms of glacial relief—various moraines and fluvioglacial trains of Pleistocene age—are somewhat different. Moraine relief, being a system of small well-drained hills, appears to be an extremely favourable biotope for the Siberian dwarf pine, which is dominant in such areas. Good drainage is provided not only by the hilly relief, but also by the very material of the moraine, consisting mostly of the products of granite weathering brought by the glacier from higher areas (Photo 16, 17). The type of the ecosystems occupying the lower areas between hills is determined mostly by the degree of water network development. The extreme case without any outflow of water leads to the formation of numerous lakes; an excellent example is the moraine adjacent to the southeastern bank of Jack London Lake, the so-called Stoozyorka ("Hundred Lakes"). In cases with some outflow the lower areas between hills are occupied by sphagnum bogs and various waterlogged sparse larch forests.

Ecosystems of watersheds. Convex watershed areas are occupied by communities without the larch. Two versions of these communities are common: with the Siberian dwarf pine and without any trees whatsoever. The ecosystems of watersheds are usually mosaic due to the uneven distribution of dwarf pine bushes, which reflects the winter wind regime of the watershed area. Snow is blown away from "wind-impact" localities, and the dwarf pine, although it is prostrate for the winter, is unable to survive in the Upper Kolyma basin unsheltered by the snow. Snow corrasion, frostburn and frost dehydration lead to the "cutting" of young shoots every winter. Thus the bushes in this area are usually "stretched" along the wind, and the closer to the edge, the more they are pressed to the surface of the soil. Thick (up to 10–15 cm) loose litter of needles accumulates under them; surface cover is either absent or represented by sparse cowberry, and lots of forest lichens sometimes grow at the leeward side of the bushes. The invertebrate community of these specific substrates is typical of forests, depleted in diversity, but quite abundant in numbers. It is dominated by centipedes (100–150 individuals of Lithobiidae and 80–100 individuals of Geophilidae per square metre); the other relatively abundant groups include spiders (100–150), diplurans (60–120), fly larvae (80–120) and rove beetles (up to 50); other animals are not abundant. Ants, which inhabit in large numbers the over-

Photo 16. On high-altitude mountain terraces (800–1000 m above sea level) peculiar communities with dominant snow lichens infrequently occur. These are usually snow-lichen larch forests. Snow-lichen communities are poor in invertebrates because of extremely small proportion of herbaceous plants, consumed by invertebrates, in their cover. The abundance of ants in these communities is extremely low.

Photo 17. At higher altitudes larch drops out, and Siberian dwarf pine forms virtually pure stand.

whelming majority of ecosystems of the mountain forest belt (see below), are almost invariably absent both under the bushes and between them.

The vegetation of the areas without the dwarf pine and between its bushes is dominated by lichen-sedge communities (*Carex argunensis, C. rupestris, Cornicularia divergens, Parmelia birulae*) with a few species of xerophile herbs (*Scorsonera radiata, Selena stenophila, Astrocodon kruhseanus* etc.); on particularly rubbly localities the lycopod *Selaginella sibirica* is abundant (Photo 18). Snow accumulates at the leeward side, leading to the appearance of mesomophic lichens, the most abundant of which is *Stereocaulon paschale*. The sedge communities, unchanging, but losing the herbs, gradually sink into the continuous layer of lichens. Further, beyond the bend separating the windward and the leeward slopes, the Siberian dwarf pine grows together with the forest biota associated with it.

The invertebrates of the sedge community are quite peculiar. Principal among them are species of the cold mountain steppes of South Siberia and Mongolia. Isolated islands of the ranges of these species are known in central and northeastern Yakutia, as well as (for some species) in other parts of the Northeast of Asia up to the upper reaches of the left-hand tributaries of the Anadyr (such as the Osinovaya River). These species include pentatomid bugs *Phimodera kibortii, Ph. laevelinia, Aelia frigida, Antheminia eurinota tamanini* and weevils *Coniocleonus ferrugineus, C. ciniritius* etc. (Berman, 1974; Vinokurov, 1979; Berman & Mordkovich, 1979 etc.). The cicadellid *Athysanella magadanica* was also found in these sedge communities; in Asia this genus in represented by two species in Mongolia and one on Wrangel Island, whereas in North America 36 species are known, including the most northern ones (Bloker & Jonson, 1987; Anufriev & Emeljanov, 1988). The byrrhid beetle *Morychus viridis*, abundant in fossil form in the Pleistocene deposits of the Northeast of Asia, is invariably present among the invertebrates of the sedge community (Kiselev, 1981; Berman, 1990). Most of the mentioned species occur at the Upper Kolyma exclusively in sedge communities; only some of them dwell also in relict steppe areas. They provide evidence of the former connection between the Northeast of Asia both with Central Asia and with North America, and the study of these species has great potential for understanding the history of the region.

Saddles of watershed areas are usually well drained and only slightly different in the pattern of their ecosystems from the watersheds themselves. If drainage decreases, the typical sequence of related events usually follows: the permafrost table rises, cryogenic microrelief is formed, and mesophile or hydrophile (in case of waterlogging) species begin to dominate in the cover.

Thus, the ecosystems of watersheds form a varied mosaic at the scale of particular bushes, clearings etc.; large-scale changes, such as those of rocks, inclination or exposure, affect their pattern only slightly.

Photo 18. Various drained areas, invariably subject to the action of squally winter winds (edges of terraces and ledges, axis parts of ranges, flat tops etc.) are occupied by cold steppe communities with dominant sedge (*Carex argunensis*). Ant nests are absent here, but carpenter ants walking in from adjacent forest communities are always abundant.

Post-fire ecosystems. All that was said above presents the principal pattern of the distribution of climax ecosystems. But the observed diversity of ecosystems is considerably greater than that, and the main factor increasing it in the sparse larch forest belt is post-fire succession.

The consequences of fires affect ecosystems differently, depending on the positions of the ecosystems (Mazhitova & Moskalyuk, 1996). Most post-fire ecosystems, resulting almost invariably from ground fires, are restored to their initial state "directly", i.e. without going through any deviating stages of succession. This is true, for instance, both of the invariably humid larch forests of the north-facing slopes and of the moderately humid ecosystems with dominant Siberian dwarf pine. On the other hand, the direction of post-fire succession on completely burned-out sites depends on many factors and often leads to the formation of long-standing ecosystems different from the original (Photo 19). For instance, burned-out lichen–dwarf-shrub larch forests with Siberian dwarf pine and alder on south-facing slopes are sometimes restored again as larch forests and sometimes replaced with aspen forests (Photos 20, 21), usually with dead cover, or with thinned dwarf-shrub cover; less often they are replaced with birch forests or with various xeromorphic herb or herb–dwarf-shrub communities.

Photo 19. In post-fire larch forests with Siberian dwarf pine small numbers of virtually all ant species present before the fire are preserved, except *F. exsecta*, since cones of its nests are, naturally, burned down.

The cause of these changes is probably the hydrothermal regime, precipitously changing after the destruction of vegetation. Temperature and water content in the upper centimetres of soil after the fire may have values equalling those of the steppe areas. The heating of the upper 20 cm layer of the soils in forest-free areas is 60–70% greater than that in forested areas. These circumstances act as control factors for a long time barring trees from colonizing open areas. The driest areas are dominated by xeromorphic sedges (*Carex rupestris, C. argunensis, C. pediformis*), the small reed-grass *Calamagrostis purpurascens* etc.

Cowberry communities, thin, but bearing abundant fruit, common and covering large areas, have mesoxeromorphic aspect. The diversity of arthropods in these communities is low due to the low water content of the soil. Only extreme xerophiles like the larvae of the click beetle *Prosternon sericeum* live between clumps of plants, others are confined to the roots of the turf. Enchytraeids are virtually absent here, but localities with high abundance of the earthworm *Eisenia nordenskioldi* (over 30 individuals per square metre) are common. In aspen forests this worm in record cases reaches an abundance of 120–150 individuals per square metre. The cause of this abundance is that
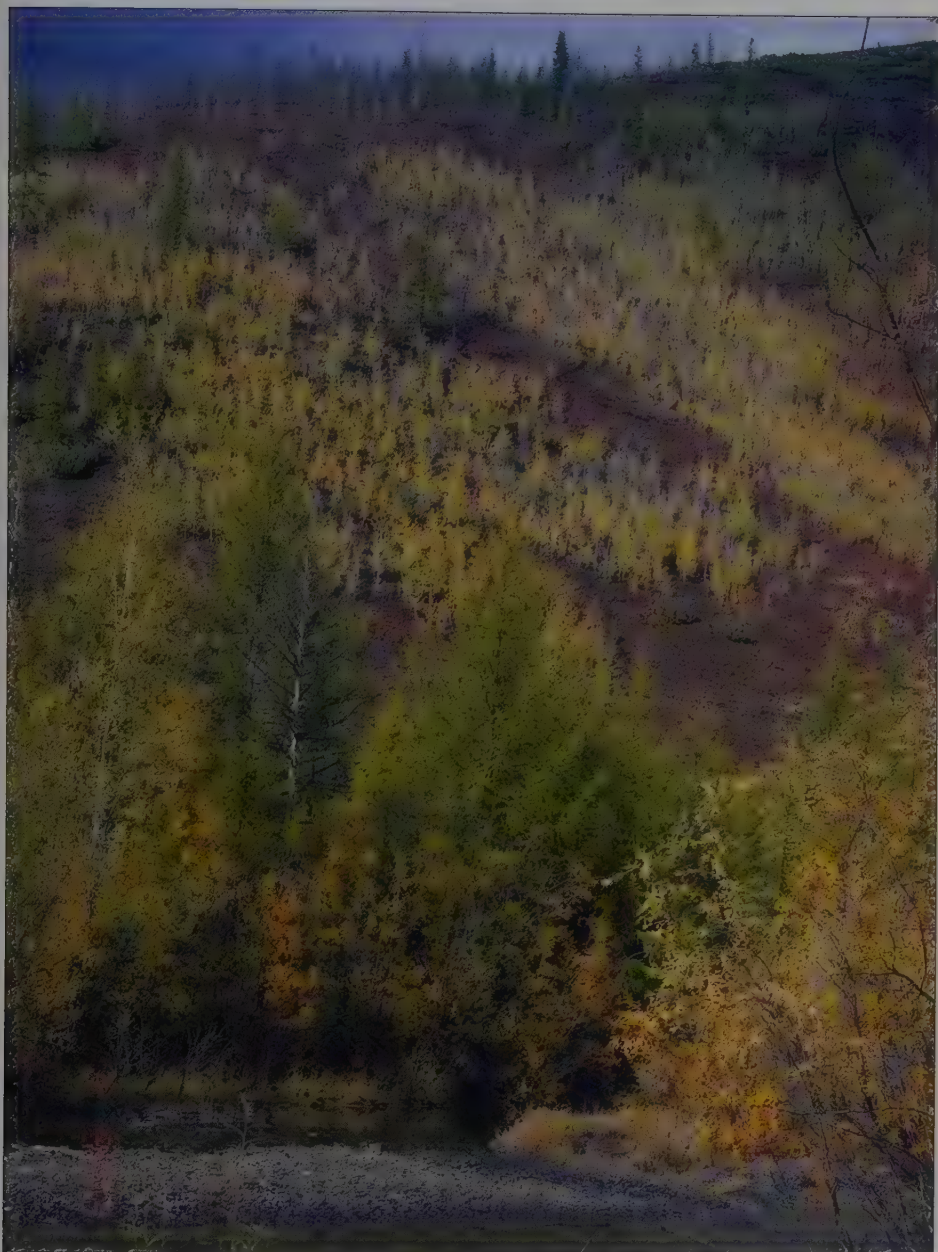
Photo 20. Only in the continental part of the region, on slopes of southern or neutral exposition, small forests of short, suppressed aspen (*Populus tremula*), distinctly standing out against the background of Siberian-dwarf-pine and larch forests by their peculiar shade of green in summer and by diversity of colours with shades of yellow and then of red prevalent in autumn.

Photo 21. Surface cover in aspen forests always has xeromorphic aspect. As in sparse larch forests of south-facing slopes, in addition to hypoarctic ants, *F. lemani* and *M. angulinodis* are common here.

aspen (*Populus tremula*) colonizes areas with somewhat better watering conditions (field water content around 20%), and its leaf litter is relatively rich in calcium, so that the pH of the soil is sometimes higher than 6. As a result, in localities with so high abundance of earthworms the upper mineral horizon of the soil is a continuous layer of coproliths.

Low humidity controls also the distribution of another taxon typical of the mineral soils of the Northeast of Asia, click beetles (Elateridae). Their abundance in the driest localities is about 20 individuals per square metre, whereas in aspen forests it is over 200 and in clearings of young birch forests over 250. However, in dense forest areas or in the more shaded mature birch forests, as well as in larch forests, the climax community of these slopes (see above), the abundance of click beetles is again as low as 10–30 individuals per square metre.

In general, the main controlling factor of invertebrate abundance in post-fire successions of lichen–dwarf-shrub larch forests on the south-facing and some of the neutral slopes is the extremely low humidity of the soil, which limits the abundance of even xerophile invertebrates (Photo 22). As soil water content increases (from place to place or in time), favourable conditions are formed for the existence of some other groups of invertebrates. However, further develop-

Photo 22. More convex slopes of southern exposition are better drained, and thus drier, larch is restoring more slowly after fires, spaces between trees are larger and covered usually with xerophyte cowberry communities with spots of dog rose and juniper clumps. Such communities are also dominated by *F. lemani*; nests of the carpenter ant are also abundant; *F. gagatoides* and *L. acervorum* build their nests in erosional depressions.

ment of organogenic horizons and of shading by surface cover or by tree canopy makes the lack of heat or the decreasing pH, both due to the accumulation of undecomposed organic materials, increasingly limiting. More humid larch forests of erosional depressions, in contrast to the successions described above, are replaced after fires by birch (*Betula platyphylla*) forests with herb cover.

The outwardly smallest post-fire changes are observed on xeromorphic, usually forest-free territories (e.g. areas of relict steppes) and after repeated fires of forest-free successional ecosystems. Fires in any circumstances doubtless contribute to an increase of such areas due to the colonization of burned-out sparse forests by xerophile plants.

Post-fire processes in the Northeast of Asia are not sufficiently studied, but it is beyond doubt that in regions with prevalent cold and monotonous ecosystems post-fire successions in most areas promote the increase of diversity in virtually every component of the ecosystems.

Ecosystems of river valleys. It is known that the floodplains of large rivers are outstanding in their peculiar hydrothermal regime due to the existence of the

so-called talik zones (Photo 23). The essence of the "talik effect" is the existence of a thawed zone between the seasonally frozen ground and permafrost. We believe that the main ecological implication of this effect is the thawing regime it creates. While springtime thawing outside talik zones spreads only from above due to conducted heating, within these zone defrosting goes both from above and from below, due to the rising level of groundwater, and during floods it continues underwater. This regime leads to the quick thawing of the entire layer frozen in winter, in about 10–15 days, which allows the existence of the entire ecosystem and in particular of the taproots of chosenia (*Chosenia arbutifolia*). Let us recall that the deepest thawing outside floodplains, observed only on extremely dry south-facing slopes (with swallow-type drainage), is no deeper than 2.5–3 m. As for the higher lowest winter temperatures of the upper layers of soil and earth in talik zones, they may equal the lowest winter temperatures of typical permafrost biotopes with similar thickness of snow outside the floodplain.

Four altitudinal levels of the floodplain are recognized, differing considerably in the type and position of their ecosystems. The lowest level, low floodplain, includes areas regularly flooded at high water and usually bearing only pioneer vegetation (herbaceous plants and young willows), usually killed by high water (Photo 24). The middle floodplain is flooded every year except in low-water years; this is the level where the proper floodplain ecosystem complex is most pronounced. Permafrost in this area is absent (as well as in the low floodplain), and mechanical impact of the flow of water is smaller, because flooding is less frequent. The middle floodplain is the area with the most pronounced chosenia, poplar and poplar-chosenia communities, the most remarkable elements of floodplain ecosystems. The forests of poplar and chosenia of northeastern Asia are quite uniform in comparison with those of the Primorye. The most common type of forest in this area is the chosenia-poplar herb type (Starikov, 1958), with undergrowth of *Rosa acicularis*, *Alnus fruticosa*, *Ribes triste*, *Sorbus sambucifolia*, *Sorbaria sorbifolia* and *Spiraea betulifolia*. The surface cover is formed by *Calamagrostis langsdorfii*, *Urtica dioica*, *Cacalia hustata*, several species of the genera *Thalictrum* and *Pirola*, etc. Another widespread type of chosenia forest is the type with dead cover in its early stages and herb cover in the mature stage. The poplar-chosenia complex occupies the principal areas of middle floodplains, whereas the Siberian dwarf pine sometimes occurs on elevations adjacent to the riverbed, and low silted areas are sometimes occupied by willow forests and sedge marshes.

The invertebrates of the poplar-chosenia communities are quite insufficiently known, but the available data indicate considerable peculiarity of their composition. In chosenia leaf litter, usually covered with silt and thus forming a kind of compost, in humid silty-sandy areas we found up to 800 larvae of small

Photo 23. Talik zones of the valleys of large rivers, floodplains with year-round underflow, are true oases among cheerless sparse permafrost larch forests and uniform, poor and impassable tangles of the Siberian dwarf pine. Chosenia and poplar-chosenia forests are a typical element of these zones.

Photo 24. Low floodplains of large rivers, flooded by high waters regularly and for long, including flooplain areas of islands, are inhabited by a specific complex of ants of two species, *M. bicolor* and *F. candida*. No other species of ants are able to dwell here.

flies and around 250 larvae of tipuloids per m²; record abundance of cantharid larvae (compared to data available in the literature), over 600 individuals m²; in addition, numerous larvae of ground and rove beetles (together around 170). This whole mass of predaceous insects exists here at the expense of abundant springtails and mites of different taxa. 30 pitfall traps set after the end of the flood (in the middle of June 1988) yielded in two months around 600 ground beetles of 15 species, by far the most abundant of which was *Nebria frigida* (330 individuals), widespread, but nowhere reaching such abundance; other species included *Pterostichus ventricosus* (145), a tundra species, *P. haematopus* (33), rare throughout the study area, and *Carabus canaliculatus* (57), one of the largest predaceous beetles in the Northeast of Asia. On the other hand, under the canopy of chosenia forests myriapods and enchytraeids are not abundant, and ants, quite numerous on the large clearings, are absent. An important feature of the invertebrate communities of the middle floodplain and the higher levels of the floodplain is the presence, sometimes in considerable numbers, of the earthworm *Eisenia nordenskioldi*, which has wide, but local distribution in the region.

The high floodplain, flooded only in high-water years, is typically covered with mixed poplar-chosenia-larch forests, where broad-leaved trees are invariably mature or ageing (Photos 25, 26). Young broad-leaved forests of the high floodplain have not been described, although we see no principal obstacles to their development. The surface cover remains the same, with prevalent herb communities.

The old floodplain, flooded only during catastrophically high waters, is everywhere occupied by larch forests, usually of the highest growth class for the continental part of the region. Poplar and chosenia are invariably absent. The cover still retains the dominance of herbs, although dwarf-shrubs and green mosses may take a visible part in its composition. Part of the territory of the old floodplain, as well as of the high floodplain, is covered with willow forests and small wetlands. In contrast to the high floodplain, the permafrost table in the old floodplain lies no deeper than 1 m. The invertebrate community is generally of transitional character. For instance, in a larch forest with *Pyrola* cover, a typical old floodplain forest, on the one hand, there are still many cantharid larvae (74 individuals per m²) and the ground beetles *N. frigida*, *P. ventricosus* and *P. haematopus*, but on the other hand, the abundance of small fly larvae and tipulid larvae is strongly decreased (39 and 8, respectively), enchytraeids appear (250), along with click beetles, harvestmen etc.

The higher terraces differ between each other in the type of their ecosystems as strongly as the levels of the floodplain. The invertebrate communities of most terraces, unlike the communities of the floodplain levels, probably have no specific features and are close to those of the ecosystems outside the valley. The ecosystems of the first above-floodplain terraces are of transitional type, strongly

Photo 25. Floodplain forests are in sharp contrast to surrounding landscapes in their peculiar flora and invertebrate fauna. The photo shows a dog-rose poplar-chosenia forest with larch in old floodplain. Because of considerable shading, only ants of the hypoarctic complex occur here, and even they only at forest edges and in large clearings.

Photo 26. Mature larch-chosenia forest in old floodplain. Situation with ants the same as in the area on Photo 25.

differing both from those of the old floodplain and from those of the higher floodplain terraces. If a terrace is sufficiently broad, it is occupied by open, often waterlogged thinned stands of larch, whereas the elevations of the fluvial relief, sometimes preserved in the terraces, are occupied by sparse larch forests. Herb–dwarf-shrub larch forests (with *Pyrola*) sometimes still occur in the better drained areas along the edges, whereas the surface cover of the main parts of the terraces is dominated by dwarf-shrubs and mosses common to zonal communities.

The invertebrate community of marshes on low banks of lakes is quite peculiar. After the flood and the following decrease in the level of lakes, the emerging sedge-sphagnum wetlands are dominated by chironomid larvae, the abundance of which is sometimes many hundreds per m^2.

The second above-floodplain terraces, if they occupy large areas and are supported by lower terraces, are also waterlogged and almost free of trees; their relief is smoothed; sedge-sphagnum bogs are common, in some cases polygonal, with large polygons and different degree of thermokarst development. Thermokarst lakes are common. On the third floodplain terrace, due to the formation of an incline towards the river, weathering processes develop, leading to the improvement of drainage and to the dominance of shrub sphagnum-sedge thinned larch stands and, on elevations and near the edges, of green-moss sparse larch forests.

* * *

The situation described above refers to the prevalent ecosystems. From among the ecosystems with small areas, but relatively rich in species composition of both plants and invertebrates, we should mention those of dry slopes, edges and ledges of terraces, where good drainage leads to the development of sparse herb larch forests with Siberian dwarf pine, dwarf pine tangles, various meadow and steppe relict communities etc. The most interesting of these communities are small areas of relict steppes (Berman, 2001), occurring on some segments of the valleys of the Kolyma and its large tributaries (Photos 27, 28). The largest of these, near the settlements Berelekh and Orotuk, occupy the area of some dozens of hectares. An important feature of relict steppes is their heating, the highest among the ecosystems of the Northeast of Asia: sums of above-zero temperatures in the first centimetre of soil are over 2500 °C. The highest temperatures at this depth in July are over 50 °C or close to 60 °C; the water content of the upper horizon of the soil at this point drops to 6%, that is, to the limit of the error of the method. These hydrothermal conditions are similar to those of the mountain steppes of southern Siberia (Berman & Alfimov, 1992). The biological diversity of the relict steppes of the Kolyma basin is considerably depleted compared to the basin of the Indigirka (Yurtsev, 1964, 1981; Berman, 1974). However, these communities include such characteristic steppe

Photo 27. The largest steppe slope of Magadan Region, near the town of Susuman (Upper Kolyma), cut by the Magadan–Ust-Nera highway. This is the favourite habitat of *F. lemani*. Erosional depression edges are abundantly colonized by *L. acervorum*; *C. herculeanus* ants sometimes walk in from the forest. In erosional depressions *F. gagatoies* and the above-mentioned hypoarctic species are abundant. In northeastern Yakutia the main part of such a slope would be inhabited by *L. muscorum*, and the periphery by *L. acervorum*.

Photo 28. Area of relict thermophyte steppe along the right bank of the Korkodon River (right-hand tributary of the Kolyma) several kilometres south of the mouth of the Bulun River. Capsules of flax (*Linum perenne*), one of rare dominants of steppe communities, are clearly visible. *F. lemani* is absent in this area, colonized by *F. candida*.

and mountain steppe species as the plants *Artemisia frigida* and *Helyctotrichon krylovii* and the following invertebrates: true bugs *Anteminia eurynota tamanini*, *Phimodera laevilinia*, *Ph. kiborti*, *Aelia frigida*, *Irochrotus sibiricus*, *Stictopleurus sericeus* and *Excentricoris pictipes*, ground beetles *Harpalus pusillus*, *H. salinus*, *H. brevicornis*, *Amara infuscata* and *Curtonotus fodina*, weevils *Coniocleonus ferrugineus* etc. In spite of the special interest of researches with different focus in the relict steppes of the Northeast of Asia, the causes of the limited distribution of these steppes and of their confinement mostly to broad river valleys are still partly unclear.

Terrace edges, although their area is always extremely small, run discontinuously for many kilometres along the valleys of large rivers, preserving xerophyte complexes from the upper to the lower reaches, which lie already in the tundra zone. We have observed fragments of such relict communities at the lower reaches of the Kolyma (Sukhaya Dresva landscape unit), at the heads of left-hand tributaries of the Anadyr (the rivers Osinovaya and Yurumkuviyem) and at the Amguema River. For instance, the invertebrates of the edges with xeromorphic sedge communities (*Carex argunensis*, *C. dariuscula*, *C. obtusata*) include a number of the mentioned steppe and mountain steppe species (true bugs *I. sibiricus* and *S. sericeus*, ground beetle *H. pusillus* etc.), also considered relict. Edges with xeromorphic communities should probably be seen as the extremely steady refuges and migration channels of the heat-loving biota.

Ecosystems of mountain tundras. The best-represented mountain tundras in the Upper Kolyma basin are those on batholiths (usually granitoid), since these elevations usually occupy greatest altitudes and often have large planation surfaces of glacial origin. The climate of the mountain tundra belt is less continental than that of the sparse forests: both the summer and the winter temperature range of the tundras is narrowed, compared to the forests, at the expense of higher temperatures in summer and lower temperatures in winter. Figuratively speaking, the temperature range of the mountain tundras is enclosed in that of the sparse forests, but their wind regime and humidification are quite different and similar to those of the zonal tundras of Chukotka.

The vegetation of mountain tundras is rather diverse. V. B. Dokuchaeva (1980) recognized 36 different plant associations in a single massif. However, most of the area of the tundras is occupied by lichen–dwarf-shrub (or dwarf-shrub–lichen) associations, not covering only the localities with extreme temperature regime or drainage conditions. These associations come up from the upper part of the sparse larch forest belt and create peculiar tundras with Siberian dwarf pine (Photos 29, 30). The dwarf pine stand is invariably thinned in these tundras due to strong winds, and its bushes stand only at the leeward

Photo 29. At altitudes 900–1100 m above sea level the mountain forest belt is gradually transformed into the mountain tundra belt. Along erosional depressions, protected from winds, larch trees reach 100–200 m higher.
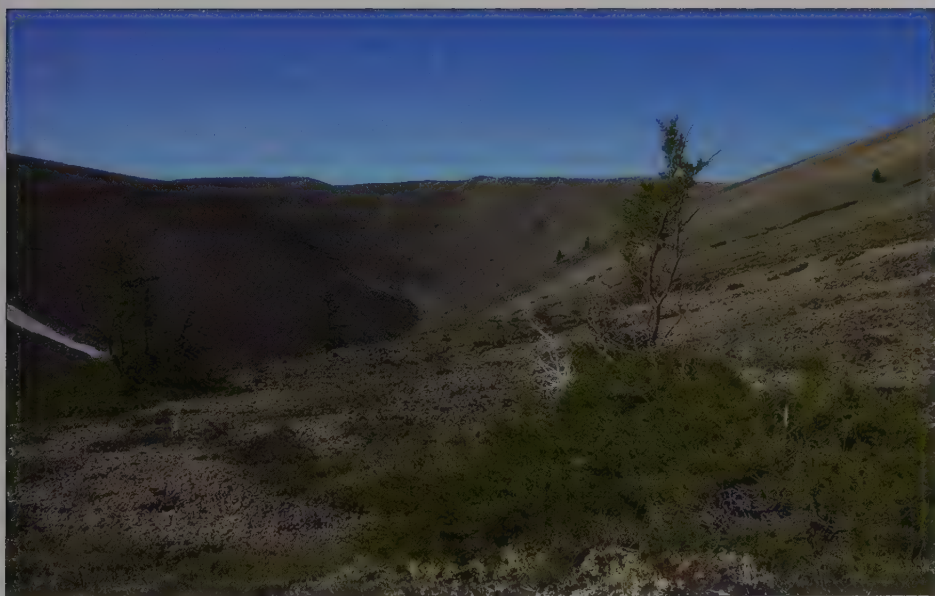
Photo 30. Creeping larch trees, developed under the effect of winter winds, climb still higher.

sides of ridges and large boulders, where snow accumulates in winter. At higher altitudes, where Siberian dwarf pine disappears, the communities retain the aspect of the areas between dwarf pine bushes, almost without changes. The cover of these communities is dominated in varying proportions by the lichens *Alectoria ochroleuca, A. nitidula, Cornicularia divergens, Cetraria cucullata, C. nivalis, C. laevigata,* and the vasacular plants *Dryas punctata* and *Phyllodoce coerulea*; at the lower levels of mountain tundras *Empetrum nigrum* and *Vaccinium vitis-ideae* are dominant; in rubbly areas the dominants are *Cassiope tetragona* and *C. ericoides*; along hollows, invariably filled with snow in winter, *Ledum decumbens* and *Rhododendron aureum* are climbing into higher altitudes.

The invertebrate fauna of mountain tundras is zoogeographically heterogeneous. Of the 105 species of different taxa (Orthoptera, Hemiptera, Coleoptera, Collembola) collected on the mountain tundras of the Bolshoy Annachag Range, 62% are widely distributed boreal species, and the remaining 38% include zonal tundra species, plain and mountain steppe species and a few conventionally endemic species (Berman et al., 1984). For instance, of the 20 ground beetles species found on mountain tundras 14 are forest species, and only 5 are more or less confined to forest-tundra and tundra (and 4 of these 5 live in the sparse forest belt). Of the 16 species of weevils (Curculionidae) found on the mountain tundras, only 2 species (*Lepyrus nordenskioldii* and *Phytonomus ornatus*) reach into zonal tundras. Of the 12 species of bumblebees, only 3 have zonal tundra distribution (*Bombus arcticus, B. hyperboreus* and *B. lapponicus*), and the rest are widely distributed forest species. Similar proportions were found in other taxa. In spite of the low number of zonal tundra and mountain steppe species, it is these species together that determine the specific character of the mountain tundra fauna. The zonal tundra species include the ground beetles *Carabus trancaticollis polaris* and *Pterostichus agonus* and the mentioned bumblebees *B. arcticus* and *B. hyperboreus*; and the steppe and mountain steppe species include the true bugs *Antheminia eurinota tamanini, Phimodera laevelinia* and *Ph. kiborti*; the widely distributed xerophiles include the springtail *Xenylla scillei*, the true bug *Emblethis brachynotus* and some other species.

The warmest and moderately humidified areas of the south-facing slopes are usually occupied by tundra meadows with such species of mesophile herbs with large flowers as gentians, anemones, claytonias etc., and with relatively rich invertebrate communities. In these areas, as on zonal tundras (Chernov, 1985), the earthworm *E. nordenskioldi* plays an important part in the invertebrate community (its abundance is up to 10 individuals per m²), absent in all other ecosystems of mountain tundras. It is along the south-facing slopes that the ants *Leptothorax acervorum* and *Formica gagatoides* species come up into mountain tundras, along with *Tetrix fuliginosa* (Orthoptera), which adds

to the orthopteran community, poor in the number of species (4), but not infrequently very abundant (1–2 specimens per m²). While the main types of mountain tundras covering subhorizontal surfaces equal in invertebrate abundance and biomass the poorest ecosystems of sparse forests, the meadow tundras of south-facing slopes are comparable in abundance to the moderately rich ecosystems, and in biomass to the richest (due, above all, to earthworms and tipulid larvae).

The other extreme of heating conditions, concave areas of the northern slopes, is colonized by green mosses and later by sphagnum, which, however, has no impact on the thickness of the seasonally thawed layer, which is deeper than 100–120 cm. The invertebrate community of these areas is also very poor and represented almost exclusively by surface-dwelling species. The relatively weak saturation of dwarf-shrub–lichen communities with herbaceous plants probably reflects rather the suppressing effect of lichens, than lack of heat or unfavourable properties of soils. For instance, on convex elements of meso- and even microrelief (*uvaly*, terrace edges, microelevations created by large rock boulders buried in the ground), from which lichens are blown off in winter, various herbaceous communities develop: in areas relatively well-humidified, meadows (similar to those described above), and in dried-up areas, sedge communities with xeromorphic sedges and sweet grass.

Both wetlands with a flow of water, often considerable in size, occupying weakly inclined areas of slopes, and small bogs with stagnant humidification, occupying saddles, occur in the mountain tundras. The vegetation of the former type of wetlands is usually dominated by large sedges and cotton grass; the soils are thawed to the depth of up to 1 m, in spite of the 50 cm layer of peat. Drainless bogs with sphagnum cover usually have extremely low depth of thawing (30–50 cm). It is remarkable that the invertebrate community of a mountain-tundra wetland with water flow has diversity of some taxa, e.g. ground beetles (15 species) and true bugs (7 species), comparable to that of pebbly dwarf-shrub tundras (16 and 10 species, respectively).

Thus, the ecosystems of mountain tundras are quite specific. Their differences from the ecosystems of sparse forests are largely explained by the pattern of the heating decreasing with altitude, which is observed only in the air, at the surface of soils and in dry permafrost soils. The gradient of the sums of average daily temperatures is about 100–130 °C per 100 m. On land with ice-bearing permafrost, where, other conditions being equal, the depth of thawing increases from sparse forests to mountain tundras, inverted heating pattern is observed, its gradient reaching 20–30 °C per 100 m. As a result, the variation of heating during the warm season decreases with height by a factor of 3–5, and both the warmest and the coldest ecosystems are found in the lower altitudinal belt.

* * *

The general outline of the spatial differentiation of ecosystems described above can be extrapolated to large areas of the mountain taiga part of the continental Northeast of Asia. Such landscapes occupy latitudinally around 8° from north to south, and the differences between the northern and the southern limits of this "zone" are less than 3 °C in average annual temperatures and 100–200 mm in annual precipitation. The floodplains in the north, still within the forest zone, may pose an important exception to this pattern. The type and distribution of the ecosystems in these floodplains may be somewhat different from those described above, since permafrost, which is thicker and colder, is preserved even in the low floodplains. Outside the floodplains, permafrost-related processes, affecting vegetation and fauna, are also more pronounced.

CHAPTER 2

ESSAYS ON THE HABITAT DISTRIBUTION, ABUNDANCE AND CHARACTERISTICS OF NEST ORGANIZATION OF THE ANTS

A total of 18 ant species are currently recorded in the vast area of the Northeast of Asia (east of the Verkhoyansk Range). Since ants, strictly speaking, do not dwell in the tundra zone (see below), this number of species refers to the forest zone of the Northeast of Asia. However, within this zone the fauna of ants is also unevenly distributed.

Species richness decreases from the Sea of Okhotsk Region to the Kolyma basin and further to the Indigirka basin. *Formica lugubris*, *F. aquilonia* and *F. fusca* have not been reported from the Kolyma Upland, whereas at the coast of the Sea of Okhotsk the former two are common and sometimes abundant. The basin of the upper reaches of the Indigirka has even fewer species of ants than the Kolyma Upland (Zhigulskaya, 1976; Zhigulskaya & Berman, 1975). *F. exsecta*, *F. sanguinea*, *F. lemani*, *F. lugubris*, *F. aquilonia* and *F. fusca* have not been found there; most *Myrmica* species currently known from adjacent areas are also unlikely to be found. The Upper Indigirka basin has only one additional species, *Leptothorax muscorum*, connected exclusively with steppe communities and absent in both the Kolyma basin and the Magadan part of the Sea of Okhotsk Region (Berman et al., 1982; Berman, 2001), but occurring on the shore near Okhotsk (Kupianskaya, 1990). By contrast, the ant fauna of Central Yakutia (Dmitrienko & Petrenko, 1976) includes at least 24 species, i.e., 10 species more than the fauna of the Kolyma basin and 14 species more than the fauna of the Indigirka basin. Central Yakutia has 14 species of *Formica*, whereas the Magadan Region has 9 (Table 2).

Thus, in the upper reaches of the Kolyma, the principal area of our study, 14 ant species have been recorded, 9 of them dominant: *Leptothorax acervorum*, *Myrmica kamtschatica*, *M. bicolor*, *M. angulinodis*, *Camponotus herculeanus*, *Formica exsecta*, *F. gagatoides*, *F. candida* and *F. lemani*. Their abundance is so high

Table 2. Ants of the Northeast of Asia and central Yakutaia.

Species	Sea of Okhotsk Region	Kolyma Basin	Indigirka Basin	Central Yakutia
Myrmica kamtschatica	+	+	?	–
M. bicolor	+	+	?	–
M. transsibirica	+	+	–	–
M. sulcinodis	+	+	–	+
M. angulinodis	+	+	–	+
M. arnoldii	–	–	–	+
Leptothorax acervorum	+	+	+	+
L. muscorum	–	–	+	+
Leptothorax sp.	–	–	–	+
Formicoxenus nitidulus	–	–	–	+
Camponotus herculeanus	+	+	+	+
C. saxatilis	+	+	+	+
Lasius niger	–	–	–	+
Formica candida	+	+	+	+
F. gagatoides	+	+	+	+
F. fusca	+	?	?	+
F. lemani	+	+	–	+
F. truncorum	+	+	–	+
F. sanguinea	+	+	–	+
F. exsecta	+	+	–	+
F. aquilonia	+	–	–	+
F. lugubris	+	–	–	+
F. pratensis	–	–	–	+
F. longiceps	–	–	–	+
F. pisarskii	–	–	–	+
F. cunicularia glauca	–	–	–	+
F. uralensis	–	–	–	+
Total	**17**	**14 (15)**	**6 (9)**	**24**

"+", presence; "–", absence; "?", highly probable; in brackets, including similar species.

that in different combinations they constitute the core of the arthropod community in most ecosystems of the region.

Considering the great differences between the physical geography and the resulting environmental conditions of the upper reaches of the Kolyma and the two adjacent regions where ants have been studied, Central Yakutia (Dmitrienko & Petrenko, 1976) and, even more so, the Primorye (Dlussky, 1967; Kupianskaya, 1990), we saw the need to give brief essays on the geographical

distribution, biotopic allocation and nest organization of the ants. *L. muscorum* is also treated in detail, because of its outstanding cold-hardiness and dwelling in the adjacent area, at the "Pole of Cold" of the Northern Hemisphere

Myrmica kamtschatica Kupianskaya, 1986

K. V. Arnoldi, looking through our collections of ants from the Northeast of Asia, noticed a species from the *M. lobicornis* group, hitherto unknown to him, considered it new and provisionally named it *Myrmica* sp. 1 (pr. *lobicornis*). This species, which long remained undescribed, was treated under this name in all our early publications (Berman et al., 1980, 1984; Zhigulskaya, 1979; Kipyatkov et al., 1984; etc.). It was later described by Z. A. Zhigulskaya (1991) as *Myrmica aborigenica* (Zhigulskaya et al., 1992; Berman & Zhigulskaya, 1996a; Leirikh & Zhigulskaya, 1999; Berman, 2001). A. G. Radchenko (1994a) synonymised *M. aborigenica* under *M. kamtschatica*, on the basis of his examination of material from Kamchatka and northern Khabarovsk Territory and our material from the Magadan Region and northeastern Yakutia, including the middle reaches of the Kolyma (environs of Zyryanka settlement). According to A. G. Radchenko, this species is similar to *M. lobicornis* in a number of characters, but closer to the Siberian species (*M. transsibirica, M. angulinodis*), and A. N. Kupianskaya's hypothesis that this species is close or even conspecific with *M. saposhnicovi* is clearly wrong. Unfortunately, A. G. Radchenko had not seen our material from the upper reaches of the Kolyma, from which *M. aborigenica* was described.

The range of *M. kamtschatica* is not completely clear. This species is known from Kamchatka, the Kuril Islands, northern Sakhalin, northern Khabarovsk Territory, but not recorded in the Primorye (Kupianskaya, 1986a, 1986b, 1990). It was also not found in the Upper Indigirka basin (our data), in Central Yakutia (Dmitrienko & Petrenko, 1976) and in Japan (Sonobe, 1977). In the Kolyma basin it was found in only three localities: at the head of the Bokhapcha River (right-hand tributary of the Kolyma in the upper reaches), in the basin of the Sibit-Tyellakh River and in the environs of Zyryanka village.

In Kamchatka, according to A. N. Kupianskaya (1986b), *M. kamtschatica* prefers humid habitats, builds its nests in the ground, under stones, in tussocks and in decayed wood. In the Upper Kolyma region it inhabits the moss and dwarf-shrub–moss sparse forests of train areas up to the altitude of around 800 m above sea level (Berman et al., 1980). The microrelief of its habitats is uneven, tussocky, formed by moss growth of different size and shape: from high tussocks to large (1.5–2 m in diameter) "pillows". The density of nests is no greater than 23 per 100 m^2, on average 5–15 per 100 m^2.

M. kamtschatica makes nests with systems of branching surface tunnels ("labyrinth") in mossy "pillows" (Fig. 4). Several large shafts (up to 1.5 cm in diameter) usually go down from the surface labyrinth, join at a depth of 15–25 cm and, widening, form 3–4 wintering chambers, each up to 25 cm³ in volume. Overwintering chambers never lie lower, probably reflecting the low summer temperatures and considerable water content of the dead moss. These chambers, connected by short and wide passages, sometimes look like a singe large chamber divided into cells. In summer, when the weather is cold, ants bring their brood into wintering chambers.

In the habitats of *M. kamtschatica* the surface of permafrost never sinks lower than 40–60 cm, even during the period of the greatest thawing (in late September). The organization of nests and the details of their structure are of major importance for living under such conditions. In spring, meltwater, the amount of which is usually small, flows between the tussocks down the still unmelted inclined surface of the train, while the central parts of the tussocks remain dry. This situation lasts over some ten days, giving the ants enough time to leave deep chambers before they can be flooded.

Small families occupy one or two chambers; large families, three to five chambers. In addition to workers, queens and exclusively third instar larvae overwinter. In the course of winter excavations the entire population of the nest was found only in the lower chambers. Overwintering workers do not form balls as, for instance, in *L. acervorum*; they cover the bottom of the chamber evenly and rather sparsely (in walking position), together with larvae, in two layers: the lower layer of larvae and the upper layer of workers. The queen is also found in the upper layer.

In each of the 20 nests excavated in winter a single queen, usually 200 to 600 workers, 150–400 large larvae and 100–150 small larvae were found. The families of this species are strictly monogynous. Only one young family during
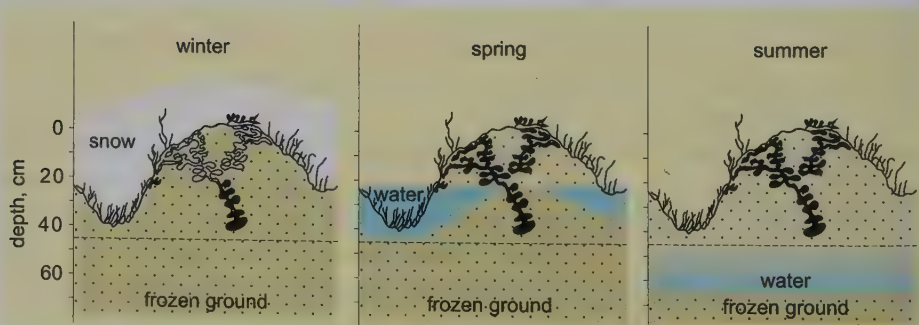
Fig. 4. Section of a *M. kamtschatica* nest in a sphagnum tussock in different seasons.

the first year of overwintering contained two queens with six larvae without workers. However, during the reproductive flight period (in August) several wingless queens were sometimes found in nests. The largest nest included 784 workers, 411 larvae and 1 queen; the smallest nest included 2 workers, 2 larvae and 1 queen. But usually the size of families and the proportion of the brood and the adults were close to those of the four nests characterised in Fig. 5.

The body length of overwintering larvae varies from 0.6 to 2.3 mm. Within these limits, their size composition can be different in different nests, some of which (Fig. 5A, 5B) contain more large larvae, whereas some (Fig. 5C, 5D) contain more small larvae. In winter the larvae have a corrugated body, flattened dorso-ventrally, with protruding lateral portions of segments ("skirtings"), considered a consequence of the winter dehydration of larval tissues (Brian, 1955).
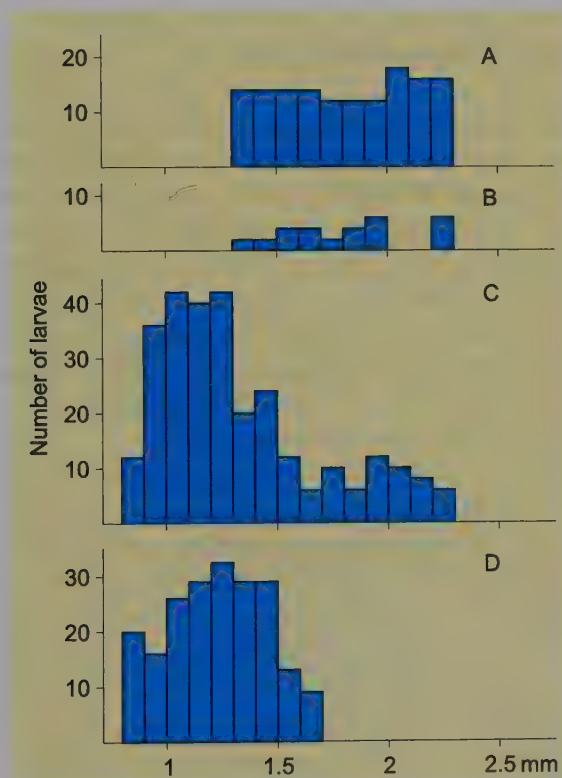
Fig. 5. Distribution of overwintering larvae of *M. kamtschatica* of different size in four nests excavated in the winter of 1985: A, no. 8513, *n* = 139 (356); B, no. 8515, *n* = 23 (148); C, no. 8512, *n* = 302 (742); D, no. 8506, *n* = 220 (520); *n*, total number of larvae shown in the diagram; in brackets, number of workers overwintering in the same nests. Ordinate, number of individuals; abscissa, body length of larvae, mm.

The size variation of overwintering larvae reflects the life cycle type of this species. Marking the larvae in summer with the vital dye neutral red, delivered with food, showed that all the larvae that have overwintered pupate during the summer only in very warm years. In normal years the smallest of them grow to a large size over the summer and overwinter again. Larvae emerging from eggs laid in spring and in summer do not pupate, but develop only to the third instar, go into diapause and overwinter for the first time. Thus, all the larvae necessarily winter at least once, and some of them (probably most) winter twice (Zhigulskaya et al., 1992). Laboratory experiments showed that in any of the tested regimes (17, 20, 25 °C with short and long daylight hours) the diapause was initiated endogenously. This is how the size diversity of wintering larvae arises.

Myrmica bicolor Kupianskaya, 1986

This species was informally recognized by K. V. Arnoldi, who looked through collections of ants from the Northeast of Asia and placed this species in the *brevinodis* group. In our publications on the fauna, biotopic distribution and cold-hardiness of ants (Berman & Zhigulskaya, 1996a; Berman et al., 1981; Zhigulskaya & Berman, 1975; Leirikh, 1989) it was called *Myrmica* sp. 2. It was described by A. N. Kupianskaya (1986b) from two localities in Kamchatka (Esso and Pushchino) and Z. A. Zhigulskaya's collections from the upper reaches of the Kolyma. "Peculiar species, clearly distinguished from the Palaearctic members of the *lobicornis* group; closer to North American species, such as *M. brevispinosa* Wheeler..." (Radchenko, 1994a: 86).

In Kamchatka *M. bicolor* prefers illuminated, warmed habitats (forest-free slopes, roadsides, clearings, cut-over areas) and nests in the soil (Kupianskaya, 1986b, 1990). We found this species in the upper reaches of the Arman River (Sea of Okhotsk basin) and in the Upper Kolyma: by the lower reaches of the Ayan-Yuryakh River near the village of the same name (at the only highway bridge in this area), by the upper reaches of right-hand tributaries of the Kolyma: the Detrin, the Bolshoy Sibirdik and the Maly Sibirdik, and by the lower reaches of the Bokhapcha, another right-hand tributary of the Kolyma. In the Magadan region, in contrast to Kamchatka, *M. bicolor* occurs only on floodplains in the same habitats as *F. candida* (see below): in sandy-pebbly areas. The nests of these species are often very close to each other, at a distance 1–2 m. They are also very similar in the type of their surface openings and in their organization. More precisely, the nests of *M. bicolor* are similar in their principal features to the single-section nests of *F. candida*. The differences are limited to

the following. In the *Myrmica* species, the diameter of tunnels and the size of chambers is smaller by a factor of 2–3, but the number of chambers, both lateral, 5–8 of which are branching in several levels from the shafts, and wintering (4–5), positioned in both species at depths of 20–40 cm, is greater than in *F. candida* (Fig. 6A). In addition, the *Myrmica* species sometimes has bunchlike overwintering chambers. But usually the chambers in both species are positioned at several levels and are shaped like bead-like widenings of the central shaft. Warming chambers are usually positioned under pebbles, preferably flat, with the size and number of nests greater under stones facing southward (Fig. 6B) than under stones lying horizontally (Fig. 6C).

All the ants in the several nests excavated in winter were distributed between 3–5 chambers at depths of 20–40 cm. For instance, one of the nests of medium size contained 428 workers, 470 larvae (0.1–1.5 mg) and one queen. The uppermost overwintering chamber at a depth of 20 cm contained 8 workers; the next two chambers, at depths of 25 and 30 cm, contained 70 and 77 workers, respectively; and the chamber at a depth of 33 cm contained 208 workers and 45 larvae. The largest of the excavated nests contained up to 1500 workers, 1000 larvae and no more than 3 queens.

The free space of the chambers and the tunnels, as in the species described here, is almost always occupied by large crystals of ice, which probably prevents the ants from drying. In spring the melting ice probably creates the humidity necessary for the emergence of the ants from the overwintering state. This hypothesis is based on the fact that in the laboratory overwintering ants could be successfully awakened only in high humidity.
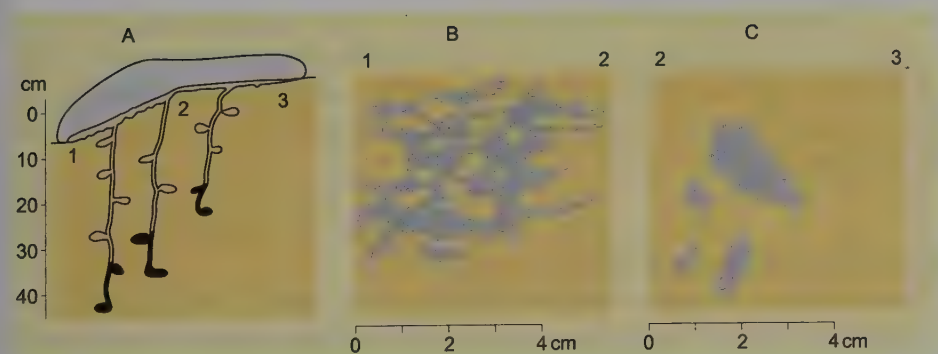
Fig. 6. Organization of a *M. bicolor* nest built under a stone (shown in gray) on a sand spit of the Detrin River. A, nest profile; sections 1–2 and 2–3 are indicated. B, projection of warming chambers under south-facing part of the stone. C, projection of warming chambers under horizontal part of the stone. Overwintering chambers shown in black.

Myrmica sulcinodis Nylander, 1846

A transpalaearctic species. Its range includes the mountains of Scandinavia, the Crimea, the Caucasus, the Urals (Arnoldi, 1968) and southern Siberia: the Western Sayan (Zhigulskaya, 1969) and the Altai (Omelchenko, 2004; Chesnokova & Omelchenko, 2005; Chesnokova, 2006); the species is also widely distributed in Yakutia, the Krasnoyarsk Territory, the Angara Region (Dmitrienko & Petrenko, 1967), the Baikal Region, Buryatia (Pleshanov, 1966), the Khabarovsk Territory, the Amur Region and Sakhalin (Kupianskaya 1990). It is abundant in the Baikal Region and in Buryatia in larch forests of all types, only rarely occurring in wetlands with suppressed larch growth. In the mountains it has been found up to 1000 m above sea level. It nests in the soil, with warming chambers under stones, litter etc.; it lives both in old stumps and under bark of recently cut larch trees (Pleshanov, 1966). In Central Yakutia it is common in cut-over areas and in larch and pine forests. The nests are underground, with excavated earth forming hills up to 10 cm in height and up to 20 cm in diameter. Nests sometimes also occur under stones, in destroyed stumps, under fallen trees. In the Podkamennaya (Stony) Tunguska basin nests in mossy tussocks are common (Dmitrienko & Petrenko, 1976).

Ants of this species from the Russian Far East were described by A. N. Kupianskaya (1990) as the subspecies *M. sulcinodis eximia*. They differ from European specimens in a number of characters, including darker colouration, and occur in the upper belt of larch and mixed coniferous–broad-leaved forests, in mountain meadows and on rocky slopes. The nests positioned among dense herbaceous plants have earthen hills, flattened in open areas.

In the Magadan Region this species is extremely rare (Zhigulskaya & Berman, 1975; Berman & Zhigulskaya, 1996a). Only a few nests were found: at the mouth of the Korkodon River (right-hand tributary of the Kolyma) and in the environs of Magadan. At the Korkodon, an entirely excavated nest on a mossy bog contained 3000 individuals; shafts reached the level of water (at a depth of about 30 cm).

Myrmica angulinodis Ruzsky, 1905

This species, which long remained unidentified, was called *Myrmica* sp. 3 in our publications (Berman & Zhigulskaya, 1996a; Berman, 2001).

The range of *M. angulinodis* includes Siberia from the Urals to the Pacific Ocean, northern Mongolia, Tuva, Buryatia, Transbaikalia, the Baikal Region, the Angara Region, Yakutia, Primorye, the Amur Region (Dmitrienko & Pet-

renko, 1976; Berman & Zhigulskaya, 1991, 1996a; Kupianskaya, 1990; Pisarski, 1969; Pleshanov, 1966; Radchenko, 1994b). A. G. Radchenko (1994a) considers this ant a typical taiga species. In the central and southern parts of Yakutia, the region closest to our study area, it is common in dry larch-pine and pine forests; together with *L. acervorum* it is one of the first species to colonize cut-over areas (Dmitrienko & Petrenko, 1976). In the Baikal Region and Buryatia it is very abundant everywhere, especially in larch forests with any degree of humidification, but rare in wetlands with suppressed larch growth (Pleshanov, 1966). In the mountains it has been found at altitudes up to 1000 m above sea level. In the Central Altai (Omelchenko, 2004) it is rare in pine forests on floodplain terraces (1–2 nests per 100 m^2) and abundant in birch forests on mountain slopes (up to 10 nests per 100 m^2).

It was found in the environs of Magadan and in the upper reaches of the Kolyma (at the mouth of the Sibit-Tyellakh River), where it has high abundance (up to 5 nests per 100 m^2) in two types of mesoxerophyte habitats: sparse herb-cowberry larch forests with Siberian dwarf pine on slopes and suppressed low aspen forests with herbaceous and dead cover. Such forests in the study area are confined exclusively to south-facing slopes in the valleys of the Kolyma and its largest tributaries; the areas occupied by these forests are small, which results in the relatively rare occurrence of this species. The nests of this ant, as well as of *Formica lemani* (see below), also colonizing these forests, are never found under bush canopy or even in its shadow, let alone in thick bush.

In the environs of Magadan, as in the Kolyma region, *M. angulinodis* occurs in the thinned areas of herb-cowberry sparse larch forests on slopes, as well as on warmed south-facing slopes with Siberian dwarf pine.

M. angulinodis builds its nests mostly in the soil, rarely under stones; these nests typically have numerous warming chambers in the upper (up to 3 cm deep) horizon and 1–2 deep (up to 40 cm) shafts ending with 2–3 large overwintering chambers. The largest of the 15 excavated nests contained 1700 workers, 800 larvae and 30 queens.

Myrmica transsibirica Radtschenko, 1993

According to A. G. Radchenko (1994), this species belongs to the *lobicornis* group and is similar to *M. bicolor* and *M. kasczenkoi* in a number of characters. A. N. Kupianskaya (1986b, 1990) identified these specimens as *M. forcipata* and *M. kasczenkoi*.

The range of this widely distributed taiga species covers Siberia from the Altai to the Pacific Ocean. Almost everywhere it prefers coniferous forests, in

the mountains reaching altitudes of 1200–2000 m above sea level (Radchenko, 1994). We found it in mixed forests in the environs of Novosibirsk, in the steppe of the Kuray depression (in the forest floodplain of the Kuray River), southeastern Altai, and in the desertificated Chuya depression (in a saline marsh).

In northeastern Asia this species was collected in mesoxerophyte larch forests of the Upper Kolyma basin (near the above-mentioned settlement Ayan-Yuryakh and near the mouth of the Korkodon River, right-hand tributary of the Kolyma) and in the larch forests of the Snezhnaya Dolina (Snow Valley) landscape unit near Magadan. In the latter locality the nests were found on the dry edge bordering a sphagnum bog adjacent to a larch forest.

Leptothorax acervorum (Fabricius, 1793)

This species is distributed in the forest zone and in the forest and subalpine mountain belts of the Palaearctic (Ruzsky, 1905); it reaches beyond the Arctic Circle into the shrub tundra zone (Dmitrienko & Petrenko, 1965; Chernov, 1966, 1975). In southeastern Asia it is common or abundant in mountain forest areas of the Okhotsk macroslope and in the basins of the Anadyr, the Kolyma, the Indigirka, the Yana (Zhigulskaya & Berman, 1975; Berman & Mordkovich, 1979).

The extreme localities where *L. acervorum* was found along the boundary of the tundra zone are of some interest for understanding the ecology of this species. We found at the lower reaches of the Kolyma as far north as the Kray Lesa (Forest Edge) landscape unit (on the right bank of the river around 100 km down from the Chersky settlement), i.e. still within the sparse larch forest zone bordering the tundra; it probably reaches several kilometres further north. V. G. Krivosheyev (personal communication) found this species in the valley of the Chaun River (Chaun Bay basin) in an area with large shrub willows and alder, approximately 10 km from the shore of the bay. In the Anadyr basin we found it everywhere along the entire routes we took from the settlements Lamutskoye and Yeropol to the mouth of the Krestovaya River (left-hand tributary of the Anadyr) and along the Mayn from its mouth to the mouth of the Algan, its right-hand tributary. In these parts of the Anadyr basin *L. acervorum* not only inhabits the sparse larch forests in river valleys, but also reaches into the peculiar shrub–Siberian-dwarf-pine tundras, prevalent here; it usually nests in remains of Siberian dwarf pine wood. Along the Bolshaya Osinovaya River it reaches up to its head, i.e. much further north than the boundary of Siberian dwarf pine distribution, into mountain tundra landscapes. Yet it occurs in these landscapes only along the dry edges of either moraine ridges or floodplain terraces, together

with a number of xerophile and steppe insects (Berman & Dorogoy, 1993). In the poplar-chosenia riparian forests of the upper reaches of the Bolshaya Osino-vaya River, we have not found *L. acervorum*, which probably reflects the flooding of these forests during high water.

This species occurs almost everywhere in the mountain forest areas of the Northeast of Asia. At middle altitudes (900–1000 m) of the upper Kolyma it avoids only extremely dry, overwetted and strongly shadowed biotopes. Formal calculation shows that *L. acervorum* is present in 35 (63%) of the 55 carefully examined areas, including dry south-facing slopes, screes, sedge wetlands and other habitats, a priori unsuitable for this species.

Since *L. acervorum* builds its nests near the surface of the soil (see below), the conditions in the 3–5 cm upper layer of soil are important for this species. It is virtually absent in steppe areas, dry grass meadows, rubbly screes and other habitats of this kind, due to the drying out of the upper horizons of the soil. Periodically flooded sedge meadows on floodplains are a typical example of overwetted habitats without *L. acervorum*. However, this species readily colonizes moss wetlands of different type (see below). It is absent both in areas with dense surface cover (such as yernik, i.e. dwarf birch scrub which in the upper reaches of the Kolyma is mainly *Betula exilis*, sometimes with a small amount of *B. nana,* but by the Sea of Okhotsk are composed mainly of *B. middendorffi* with small amounts of *B. exilis.*) and from forests with dense canopy (dense larch forests, mature birch and alder forests etc.) (Photo 31). But *L. acervorum* is not completely absent in these communities. The development of slightly milder conditions is enough for this species: it occurs at edges of steppe areas; under fallen trees on screes; on hillocks in sedge wetlands; in small clearings in yerniks, Siberian dwarf pine tangles and larch forests. Moreover, the density of its nests in such areas is sometimes quite high (1-2 per m^2). Generally, the proportion of middle altitude areas without *L. acervorum* is very small. In most biotopes the average density of its nests is 5–20 per 100 m^2, but in sparse sphagnum larch forests, widespread on valley bottoms and on the south-facing slope trains of the Upper Kolyma region, their density reaches 40–50 per 100 m^2 (Photos 32, 33, 34). In some areas of such thinned tree growth with pronounced undulate relief formed by sphagnum "pillows" (tussocks), the nests of this species are extremely abundant: on the average no less than 1, and up to 3 per m^2.

At altitudes of 900–1100 metres above sea level *L. acervorum* avoids northern slopes and flat tops of ranges; the density of its nests on west- and east-facing slopes dramatically decreases compared to that of the lower altitudes. Along south-facing slopes this species reaches an altitude of 1400 m.

This description of the biotopic distribution of *L. acervorum* shows that the Upper Kolyma region is close to the optimum of its range. In this area the spe-
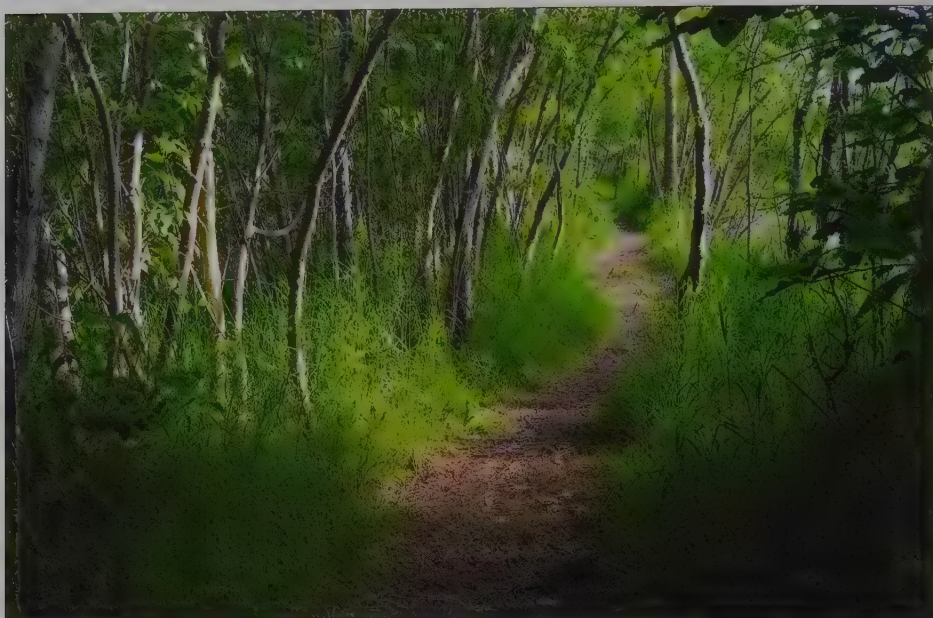
Photo 31. Young alder forest with birch and willows on a small brook terrace. Deep shadow and ants are incompatible.

Photo 32. Post-fire area, approximately 15 years old, of an east-facing slope (500 m above sea level): perfect place for hypoarctic ants. Landmarks with red tops, indicating only *L. acervorum* nests, give the idea of ant abundance.

Photo 33. The same area in summer. Distant steep slope of southern exposure is covered with light clumps of young aspen to the left and young larch-birch forest to the right; all forest-free area is occupied by nests of *F. lemani*. Upper and left parts of the slope are covered with Siberian dwarf pine communities.

Photo 34. Grounds of a gently sloping train with sparse larch forest with moss–dwarf-shrub cover thawed by late June less deep than 30 cm. However, this is no obstacle to colonization by hypoarctic ants, and in drier and more raised areas, also by *F. exsecta*.

cies has almost the highest density recorded in the literature and in our data, and occupies an extremely wide range of habitats. For comparison: in the forests of the southern and middle taiga of West Siberia and the southern taiga of East Siberia, studied by Z. A. Zhigulskaya and L. V. Omelchenko (1977), this species occurs in few biotopes (mostly waterlogged and cut-over areas) and the density of its nests is never higher than 10 per 100 m². Similar results were reported from the North, Middle and South Urals (Gridina, 2003), Middle Volga Region (Astafyev, 1971), Tuva (Zhigulskaya, 1968), Baikal Region (Pleshanov, 1966) and Primorye (Kupianskaya, 1975a, 1975b, 1990). In Central Yakutia (Dmitrienko & Petrenko, 1976) and in the northern taiga of the Ob valley (Omelchenko & Zhigulskaya, 1981) *L. acervorum* is also widely distributed, but its highest density is no greater than 12 nests per 100 m². According to V. Z. Rubinshtein (personal communication), the average density of this species in the North Urals in 17 examined biotopes (from plain light coniferous taiga to mountain tundras) usually falls within the interval of 0.1–1.0 and only in some cases reaches 2.1 and the maximum 5.25 nests per 100 m² (the latter value refers to cowberry–lichen–green-moss pine forests); and the record density of its nests was found only in some sampling areas in the light coniferous taiga of the Pechora Region (lichen–green-moss pine-cowberry communities), equivalent to 20–30 nests per 100 m².

All the types of *L. acervorum* nests known from other parts of its range occur in our study area, with the exception of the type found by A. A. Zakharov (personal communication) in the canopy of trees on the Kola Peninsula. It is known that the nests of *L. acervorum* have a primitive structure and are built under some kind of cover (such as flat stones no thicker than 2–3 cm, remains of wood, animal faeces etc.), directly in the soil, in wood (in roots, at the base of standing tree trunks, in fallen trees etc.), in moss and in other substrates. In all these cases the nests retain the same extremely primitive outline of structure (Fig. 7a): numerous warming chambers and tunnels directly under the cover or the surface, densely penetrating the upper layer of the substrate (1–3 cm). A shaft ending in a large chamber of about 2 cm³ and used both in summer and in winter usually goes down from the surface labyrinths. But details of nest structure greatly vary under different conditions, and considering these details is useful for understanding particular adaptations, in some cases seemingly unimportant, but together providing the extremely wide ecological lability of this species.

Nests in larch wood are positioned in dead parts of the trunk base, in roots protruding from the ground and in fallen trees and stumps. They are peculiar in the proximity of the tunnels to the surface: usually no deeper than 1–2 cm. The tunnels are built along the surface of the wood and used as warming chambers; the vertical shaft is virtually absent, and the overwintering chamber is not

deeply embedded in the wood (Fig. 7b). Somewhat more complicated is the structure of nests in thin branches: they contain warming chambers penetrating the entire diameter of the branches, and the overwintering chambers are built in the soil under the fallen tree (Fig. 7c).

Nests under flat stones, usually no thicker than 2–3 cm, are very common. These stones are quickly heated and retain their heat for a relatively long time. Warming chambers, reaching the size of up to 20 cm³—huge for this species, are positioned immediately under the stone. On dry slopes of southern exposure the shaft under the warming chamber is usually strongly widened along its entire length; short tunnels branching from the shaft lead to lateral chambers, forming the second level, where ants bring their brood during hot weather. Nests of large families sometimes have more than one shaft under the warming chamber, also with a second level of warming chambers (Fig. 7d). The second level can be well developed in nests using as the cover not stones, but bark, wood chips, dry dung, pieces of plywood etc. These materials are quickly heated, but have lower heat capacity than stone and thus not so efficient for maintaining the temperature in the nest.

Nests in moss are diverse, and their organization depends on their position, age, type of moss and soil etc. Details of nest organization in moss are more visible during winter excavations, because all the tunnels, even the smallest, appear as if they were laboratory preparations due to the ice crystals that fill them, whereas in summer they are hard to distinguish against the background of the lax structure of wet moss. The most interesting features of nests in moss are described below.

Moss nests, unlike nests under cover, almost never have large warming chambers, but the tunnels themselves in the layer 0–0.5 cm deep form miniature networks between the fronds of moss, often opening directly into the illuminated surface (Fig. 7e). The density of tunnels in this layer is so great that the distance between them is smaller than their diameter. In early spring, during the first sunny days, ants warm their larvae in these miniature networks, sometimes bringing them out onto the moss, under direct rays of the sun. Nests often have the form of 2–3 surface cup-like chambers connected with each other, with one downward shaft, widening at the end (Fig. 7f).

It happens rather often that a mature nest in moss is accidentally covered with a fallen alder or birch leaf, which leads to a dramatic decrease in illumination and heating. In such cases the ants do not abandon their nest, but use the space under the leaf as a warming chamber (Fig. 7h).

On wet moss cover ants will, if it is possible, build warming chambers in any material lying on the surface: pieces of wood, branches, bark, dry dung etc. Rather often nests are built in dense spherical growths of the moss *Dicranium*

Fig. 7. Sections of typical nests of *L. acervorum* in the Upper Kolyma area. Nests in soil, background clear; nests in moss, background dotted. Overwintering chambers are shown in black. For further explanations, see text.

elengatum Lehleich. (Fig. 7g), 5–8 cm in diameter, connected with the main surface by a "stem", through which runs the shaft leading to wintering chambers, lying, as usual, near the surface of the soil. The inner part of the sphere is usually perforated by tunnels, the total capacity of which is close to a quarter of the sphere's capacity. The conditions in such spheres are relatively favourable, because the spheres are remote from the wet and cold substrate. It is no coincidence that of 1578 examined spheres 70% contained inhabited nests of *L. acervorum*, and the remaining 30% had well-preserved tunnels. Only on steep northern slopes are such spherical moss growths not occupied by ants.

Nests on southern sides of large sphagnum tussocks (Fig. 7i) are similar to those described above (see Fig. 7a), differing from them only in the position of the tunnel leading to the overwintering chamber, which runs almost parallel to the surface of the tussock. Thus, the family winters no deeper than 2–3 cm from the surface.

Nests in tussocks with dying sphagnum cover, where capillarity is disrupted, resulting in a very dry upper layer of moss and relatively humid deeper layers (from 3–5 cm deep), have a peculiar structure. Nests on such tussocks have an extremely wide (0.6–0.8 cm) entrance, immediately leading into an inclined shaft with small lateral chambers and disproportionately enlarged terminal part (Fig. 7j).

As we have noted above, the greatest density of *L. acervorum* nests was observed in dwarf-shrub–sphagnum sparse larch forests of gently sloping trains with distinctly pronounced nanorelief. Detailed mapping of nests, carried out here along transects 20 m long and 2 m wide, revealed a number of important features of their allocation. *L. acervorum* is capable of finding in biotopes generally unsuitable for its existence minute plots of the nanorelief with summer microclimatic conditions favourable for a nest, often in spite of poorer conditions for overwintering. This is possible, on the one hand, due to the considerable cold-hardiness of this species (which allows it to display indifference to overwintering conditions), and on the other hand, due to the small size of the nest, where the projection of the tunnels has the area of only 0.1–0.5 dm². All the nests we found, not only of *L. acervorum*, but also of *M. kamtschatica* and of *F. gagatoides* (see below), were confined exclusively to projecting elements of the nanorelief: separate tussocks, "pillows" (Fig. 8), fallen tree trunks and large branches covered with moss.

Most *L. acervorum* nests built on terraces and other subhorizontal areas and especially on northern macroslopes face southward, due to the same tendency to build nests at the top or at the southern side of tussocks: of the 127 nests of *L. acervorum* recorded along the transects, 68% were at the top of the tussock, 25% on the southern side, and only 2–3% on the eastern and the western side of the tussock; on the northern side no nests were found.
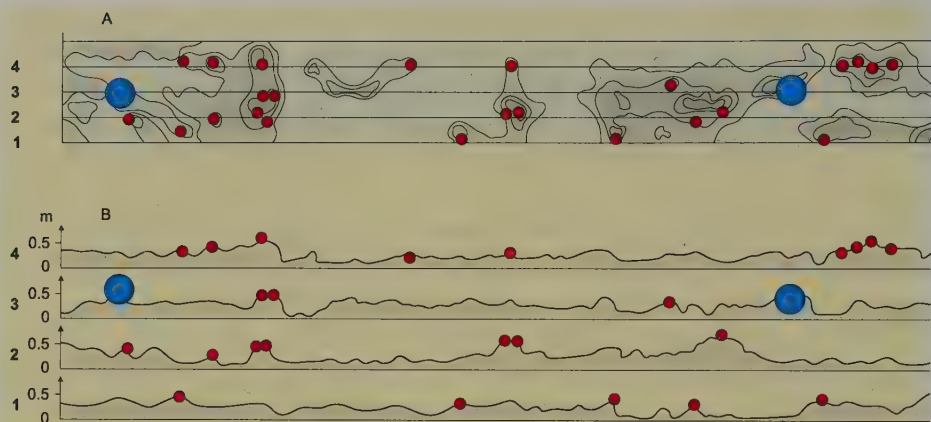
Fig. 8. Distribution of nests in different microrelief elements in a sphagnum larch forest. A, plan of the transect 20 m long, 2 m w; B, profiles of a series of vertical cuts of the transect (1, 2, 3, 4) made every 50 cm. Red circles, nests of *L. acervorum*; blue circles – nests of *M. kamtschatica*; orange circle, nests of *F. gagatoides*.

Finally, another peculiar feature of nest location is the distinct preference within the described tussocky area for localities with dense moss cover (without dwarf-shrubs or sedges) and for half-decayed stumps and other remains of wood buried in moss.

The prevalent nest type in particular biotopes depends on many factors. In habitats with sphagnum cover ants build their nests only in the moderately humid "pillows". On northern slopes they nest in tussocks, in hillocks by tree trunks, in roots protruding from the surface, in the bark at the base of trunks, in stumps etc., but, as noted above, virtually always on the side facing southward. In habitats with mineral substrate ants prefer nesting under flat stones, and in their absence, in remains of wood. At higher altitudes nests are more often found under stones, and in the mountain tundra they occur exclusively under stones. In general, from the valleys to the higher altitudes, along with a trend towards habitat change (Bei-Bienko, 1966), a decrease in the number of nest types is observed.

The brief review of nest organization given above shows that in markedly different ecological conditions this ant species, in spite of its primitive nest construction, uses a wide array of building techniques, generally aimed at conditioning, above all, the temperature, but always preserving the humidity. Dry areas with fine material, especially on south-facing slopes, are very strongly heated: the temperature sometimes reaches 55–60 °C at the surface of the soil and 25–30 °C at a depth 5–10 cm (Berman et al., 1982). In other words, the

layer of soil inhabited by *L. acervorum* is usually more than adequately heated, but it is mostly too dry for this species. Thus, habitats favourable in temperature are unsuitable in humidity, and *L. acervorum* is forced to colonize humid, but insufficiently warm areas, modifying the position and structure of its nests.

The mentioned position of most nests on the southern side of the upper part of the tussock results also from necessary avoidance of flooding by percolating meltwater runoff and from the thermal advantage of this position: the southern side of the tussock gets 10% more heat during the warm season than the surface of its horizontal part (Table 3). However, this heat is strongly transformed in the horizons of the tussock below the surface. The heat-insulating properties of mosses are well known; the seasonal thawing on northern slopes under the cover of sphagnum in our study area is no deeper than 50 cm (and no less than 30 cm), and in the dwarf-shrub–moss larch forests on the trains of southern and eastern exposure it is no deeper than 60 cm (from the base of the tussock). As a consequence, considerable vertical temperature gradients develop within the moss cover. On sunny days the temperature at the surface of the moss reaches up to 32–35 °C, whereas at depths of 50–60 cm (the surface of permafrost) it remains close to 0 °C for 24 hours. Particular patterns of temperature distribution vary,

Table 3. Ranges and sums of temperatures in different parts of a sphagnum tussock, in a horizontal area and in the air, 21–30 August 1981

Sensor no.	Sensor position	Range of temperatures (lowest–highest)*, °C	Sum** of t > 0 °C	Gain of heat*** (%)
1	Air	4–24	996	6
3	Tussock, southern side, surface	2–34	1043	11
4	Tussock, southern side, 5 cm	1–18	965	12
10	Tussock, centre, surface	2–28	938	0
11	Tussock, eastern side, surface	1–24	931	−1
9	Tussock, western side, surface	1–25	902	−4
8	Tussock, northern side, surface	2–20	829	−12
12	Tussock, centre, 15 cm	8–13	823	48
13	Horizontal area, surface	2–27	937	0
2	Horizontal area, 5 cm	2–15	862	0
6	Horizontal area, 15 cm	6–8	555	0

Notes.
* Extreme values according to measurements taken every 3 hours.
** Sum of temperatures according to measurement taken every 3 hours.
*** Gain of heat compared to the same depth in the horizontal area (%).

depending on the colour of the moss, its density, humidity etc., but the principal feature remains constant: the strongest gradients are observed in the upper 5 cm (Fig. 9). In this layer highest daily temperatures (as well as annual sums of average daily above-zero temperatures) may decrease by the factor of two. However, at the surface of the tussock not only the highest daily temperature is higher, but also the lowest daily temperature is lower than in the horizons lying below the surface. Therefore, ants can avoid overheating, escape from the low night temperatures and very effectively collect heat by moving only within the upper layer (0–5 cm deep). The sum of temperatures higher than 10 °C to which the individuals performing such movements are exposed may be 16% greater than
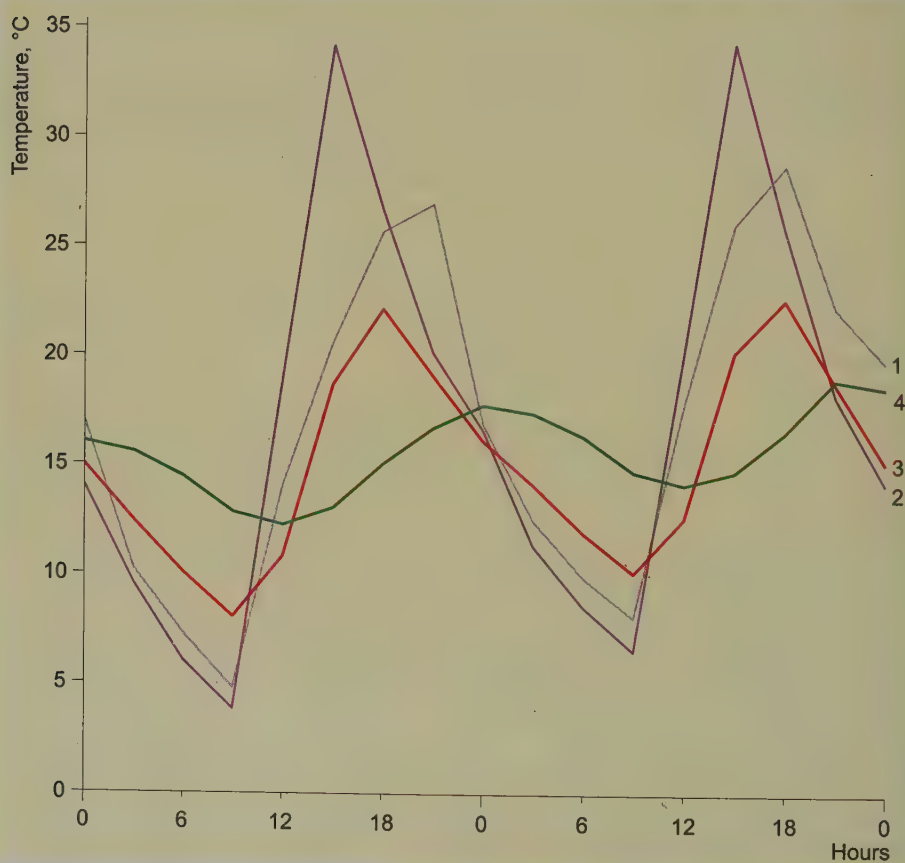
Fig. 9. Daily range of temperature in the air and in different parts of sphagnum tussock during the warmest summer days (24 and 25 July 1980). Temperatures: 1, in the air; 2, in the surface horizon (depth 0–1 cm) of the southern side of the tussock, 3, in moss on the southern side of the tussock at the depth of 5 cm; 4, the same, depth 15 cm.

the same parameter in the upper cm of the soil and over 30% greater than at the depth of 15 cm. The highest temperature of the surface of the moss at the southern side of a sphagnum tussock is sometimes 15–20 °C higher than the air temperature and 10–15 °C higher than the temperature of the upper cm of the soil of the even part.

The chance to collect additional heat by performing, together with the brood, vertical migrations within the nest, following the optimal temperatures for 24 hours, also contributes to the well-being of this species. Although the vertical size of the nest is rather small, the differences in temperature and humidity between the warming chambers and the deepest chambers are considerable. The described pattern of temperature distribution in the moss at constantly high humidity is very important for invertebrates: moving by a few centimetres, they can choose the temperature they need within a very wide range. Obviously, even the seemingly smallest variations in nest organization, especially in the structure of warming chambers, are of use to ants for these migrations.

Although such temperature differences are observed only during sunny days, their contribution to seasonal sums of heating is considerable, since the proportion of clear days in continental areas of the Northeast of Asia is high. In the upper and the middle reaches of the Yana, the Indigirka and the Kolyma, the total number of sunshine hours in the period from May to August reaches 1000–1100, which is only 50–100 hours less than in the Crimea (Spravoch-nik..., 1966). Generally during the warm season ants can get approximately 20% more heat than the horizontal surface (or 14–15% higher sum of temperatures than recorded in the air) due to the southward nest position and to the vertical movements within the nest. There are reasons to believe that the value of this addition is still greater (30–50%) due to the fact that ants can move together with their brood not only vertically (between day and night), but also within the warming chambers, following the sun, i.e. in the east–south–west direction.

The facts presented above show that the organization of nests with overwintering chambers near the surface of the soil enables the ants to maximise their exploitation of the climatic resources to allow them to complete their life cycles successfully. They achieve this not only through heat collecting by daily movements discussed above, but also through the prolongation of the warm season, which is no less than two weeks, and sometimes up to one month longer than in the horizon 15–20 cm deep. As we noted above, this strategy is possible only in insects with considerable tolerance to winter cold, since the lowest soil temperatures are observed, naturally, in the upper few centimetres. *L. acervorum*, as will be shown below, is one of the most cold-hardy species.

Thus, unlike large *Formica* nests, where ants condition temperature and humidity (Dlussky, 1975; Bachem & Lamprekht, 1983), in the nests of *L. acer-*

vorum the environment is optimised by choice of nest position and by moving within the nest to the currently most favourable localities. Generally, the lability of nest-building and "thermophile" behaviour doubtlessly contributes to the wide habitat distribution of *L. acervorum* (Berman et al., 1987b).

However, all the adaptive features of nest building described above cannot guarantee completing development in one season. Measurements and calculations show that in favourable years there is enough heat for complete development in the Upper Kolyma basin, but in years with high summer precipitation the sums of temperatures may remain below the threshold value. But at the northern boundary of the range, as well as at the upper altitudinal boundary, there is not enough heat for completing the life cycle even in favourable years. The sum of above-zero air temperatures at the Aborigen Field Station reaches 1600 °C in the warmest years (with average annual sum of above-zero temperatures 1350 °C), while at the Rytkuchi Meteorological Station (southeastern coast of the Chaun Bay), which represents the climatic conditions near the northern boundary of the range, this sum reaches only 714 °C (Spravochnik…, 1966). Therefore, the endogenous diapause regulation in larvae, which provides the prolongation of the brood's development cycle at least to two years and thus guarantees successful reproduction, is an important adaptation to such climatic conditions (Zhigulskaya et al, 1983; Kipyatkov et al., 1984).

Clear evidence of this can be observed in late autumn in the composition of any family of *L. acervorum*. The nests of this species, in addition to overwintering queens (in 50 excavated nests we usually found only one queen, rarely two or three, and only in one nest eight) and workers, which constitute from half to two thirds of the family, invariably contain larvae of different size, their weight varying from 0.2 to 2.5 mg. The size of the larvae largely reflects their chronological age, and not their instar, as in *M. kamtschatica* (see essay above). All the larvae invariably overwinter at least once, some of them require second overwintering, and in the experiments of T. A. Kipyatkova (1987) some individuals completed their life cycle only after overwintering three times.

The total number of individuals in most overwintering families varied from 50 to 100; the largest family contained one female, 126 workers and 150 larvae (18 large, 70 small, the rest of medium size).

Thus, the well-being of *L. acervorum* in the extreme conditions of the Northeast of Asia depends on a number of adaptations, providing (1) optimal consumption of heat (southern position of nests and daily movements within the nest following optimal temperatures), (2) brood vitality preservation during cold summers, when heat is lacking, and prolongation of development to 2–3 years, (3) capability of overwintering at low temperatures (physiological mechanisms of cold resistance). These adaptations help *L. acervorum* to profit from

living near the surface of the soil by awaking early in spring and thus using as much as possible of the heat resources of the climate.

Leptothorax muscorum (Nylander, 1846)

L. muscorum is a boreal species distributed in North and Central Europe, in the Caucasus and in Siberia from the Urals to the Primorye (Ruzsky, 1905). It is recorded in the Altai (Omelchenko, 2004; Chesnokova, 2006), in the Baikal Region (Pleshanov, 1966), in Tuva (Zhigulskaya, 1968), in the Krasnoyarsk Territory, in Buryatia, in southern and Central Yakutia (Dmitrienko & Petrenko, 1976), in the Chita Region, in the Khabarovsk Territory, in Primorye, in Sakhalin, in Kamchatka and on the coast of the Sea of Okhotsk near the city of Okhotsk (Kupianskaya, 1986b, 1990). An isolated part of the range was found in the Upper Indigirka basin (Zhigulskaya, 1976; Berman et al., 1982; Berman, 2001).

L. muscorum inhabits extremely diverse biotopes within its range and is relatively rare everywhere (Ruzsky, 1905). It prefers thinned-out broad-leaved forests in North and Central Europe and pine, larch and birch forests in the Urals, where it reaches the summits of mountains (Ruzsky, 1905) and occurs in cut-over areas and clearings in forest-steppe and in steppe (Gridina, 2001, 2003). In West Siberia it colonizes dry biotopes: pine forests in valleys and interfluves and cut-over areas recent and overgrown with young trees (Zhigulskaya & Omelchenko, 1977); in the northeastern and central Altai it was recorded in low birch-aspen forests (Omelchenko, 2004; Chesnokova & Omelchenko, 2005). In East Siberia, Yakutia (Dmitrienko & Petrenko, 1976) and the Baikal Region (Pleshakov, 1966) it is found in larch and pine forests and in cut-over areas. In Tuva it occurs at forest edges, but also in steppe plains at the foot of the mountains and in steppes on mountain slopes (Zhigulskaya, 1968). In the Russian Far East it is a forest species, but with a preference for thinned-out forests and cut-over areas; in the northern Khabarovsk Territory, near the settlements Ayan and Nelkan at the coast of the Sea of Okhotsk, it was found in pine forests (Kupianskaya, 1986b, 1990). However, in northern Yakutia this species is confined exclusively to the areas of relict steppe. Thus, in the more northeastern parts of its range, *L. muscorum* shifts towards drier and warmer habitats, and beyond the Verkhoyansk Range it inhabits only steppes, and does not occur even on steppe meadows (Berman et al., 1982).

The abundance of *L. muscorum* at the Indigirka varies considerably depending on the position of steppe areas, their size, incline, microrelief, amount of rubble in the soil, and projecting cover of the vegetation. While *L. muscorum* is rare everywhere within the main part of its range, in the Oymyakon depres-

sion it is abundant: up to 2–3 nests per m². In this depression the nests of *L. muscorum* were found not only on slopes of southern exposure, but also on west- and east-facing slopes, which it colonizes following the steppe vegetation. In the Nera valley the density of nests in the steppe areas is lower, in spite of the presence of seemingly suitable habitats. *L. muscorum* does not colonize small (up to 0.5 ha) islands of steppe surrounded by forest. It is absent on steep slopes (30–40°), unturfed and with unstable ground. In large steppe areas it occurs almost everywhere, avoiding only especially dry and heated parts of the slope (usually on convex relief elements), localities with dense vegetation (such as thick undergrowth of *Artemisia gmelini*) and communities with thick turf (projecting cover over 70%) produced by grasses. High density of nests (1 per m²) was observed on gentle (up to 20°) rubbly slopes. On debris cones and in erosional microdepressions on gentle slopes retaining steppe vegetation the density of nests sometimes reaches 2–3 per m². *L. muscorum* does not go under forest canopy, but colonizes also steppe edges, where *L. acervorum*, *Camponotus herculeanus* and *Formica gagatoides*, in their turn, come from the forest. All the four species are often found within several square metres in such localities. Yet this zone is narrow (2–5 m) and shows especially distinctly in the distribution of *L. muscorum* and *L. acervorum*: the abundance of the former increases towards the steppe, and the abundance of the latter increases towards the forest or the wetland adjacent to the debris cone. These species display a similar distribution pattern around isolated larch trees standing in steppe areas.

In the Oymyakon depression, distinguished from all the other depressions of the Northeast of Asia by the most continental climate, truly arid conditions have developed. The average annual precipitation in this depression is no greater than 175 mm; the radiation aridity index is over 2.0, which is characteristic of zonal deserts (Buks, 1977). The daily course of the radiation balance in slope steppes of the upper reaches of the Indigirka is distinctly asymmetrical, due to the increased radiation of the heated soil surface in afternoon hours, which is also typical of semidesert and desert areas. While the average monthly air temperature in July is 15 °C (and the highest July temperature is 33 °C), the temperature of the soil surface in slope steppes on convex, steep and weakly turfed localities sometimes reaches 60 °C. According to our data (527th km of the route from Khandyga to Magadan, 30 June to 5 July 1979), the average temperature of the 40 cm layer over four days was 18.1 °C, with the highest temperature at the surface reaching 58 °C. As a result of such high temperatures, the soil dries out almost completely (with humidity as low as 1.4–3.4%) and permafrost table lies deep. On northern slopes, in larch forests adjacent to steppe areas, soil temperature is considerably lower, only 2 °C at a depth of 2 cm, and humidity, due to the proximity of permafrost, is close to 100%: water oozes

from the soil (our data, 527th km of the route). Areas bordering the steppe, especially slope-trains and erosional depressions, where the *L. muscorum* reaches its greatest abundance, probably provide the combination of not too high temperatures and sufficient humidity (at least 5–7%) required by this species. The above-described ecological requirements and biotopic allocation of *L. muscorum* indicate its poor potential for dispersal beyond steppe communities.

In the Indigirka basin *L. muscorum* nests only under flat stones (Fig. 10), whereas in the main part of its range it builds nests in extremely diverse substrates: in remains of tree trunks and branches, in stumps, under pieces of bark, in earthen tussocks and under stones (Ruzsky, 1905). Of the 1052 nests we found on 50 steppe areas in different parts of the Indigirka basin, only one was under a piece of Siberian dwarf pine bark, and five were under old horse dung. All the nests are of the same type and simple in structure. Directly under the stone there is a large, up to 1 cm³, chamber for warming the brood, from which a single shaft, sometimes with 1–2 side branches, goes down and usually ends at a depth of 7–10 cm in a single overwintering chamber no larger than 0.5 cm³. As winter excavations showed, the shaft and the overwintering chamber are tightly packed with workers (20–100), together with queens (1–5) and small and large larvae (20–70). The proportion of small and large larvae varies from nest to nest, reflecting differences in the number of times the brood has overwintered (see the essay on *M. kamtschatica*). Winged individuals do not usually overwinter: of the 40 nests excavated in winter, only one contained a winged queen, which, as its successful awakening showed, safely survived overwintering.
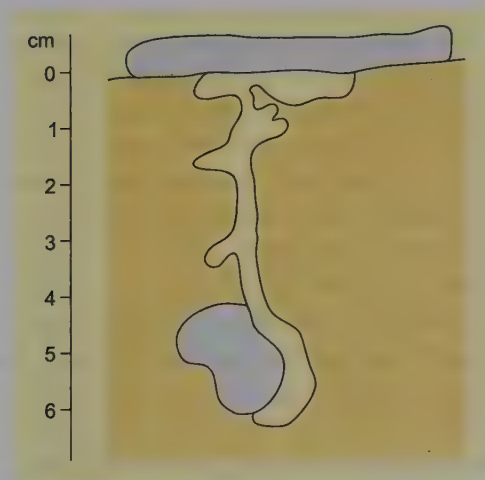
Fig. 10. Section of a *L. muscorum* nest built under a stone on a south-facing steppe slope. The lower chamber surrounds the stone (shown in gray).

The inside of tunnels and chambers free of ants, including the warming chamber, is filled with ice crystals over the whole winter, in spite of the low humidity of steppe soils.

Camponotus herculeanus (Linnaeus, 1758)

C. herculeanus is a Holarctic forest boreal species (Arnoldi, 1968). In the Urals it occurs mostly in the northern part (Rubinshtein, 1971; Seima, 1969, 1971; Gridina, 1998, 2003). In the forests of Central and East Siberia (including the Krasnoyarsk Territory, the Angara Region, the Baikal Region and Central Yakutia) it occurs everywhere, but has low abundance (Pleshanov, 1966; Dmitrienko & Petrenko, 1976; Zhigulskaya & Omelchenko, 1977). In all these areas high density of nests (up to 1 per 100 m²) is observed in cut-over areas, post-fire ecosystems and mixed interfluve forests.

In the Northeast of Asia it is invariably present in forest communities, including Siberian dwarf pine and larch forests. In the upper reaches of the Kolyma it occurs from the floodplain to mountain tundras (Berman & Zhigulskaya, 1987, 1996a; Berman et al., 1980). In the sparse forest belt up to the altitude of 900 m above sea level it is present everywhere on slopes of any exposure, avoiding only rubbly, strongly dried-out areas of south-facing slopes and sedge wetlands. It prefers larch forests with mesophyte surface cover.

The position of nests depends on the availability of suitable places for building them. In most habitats there is 1 nest per 100–400 m², but densely populated areas (with 3–4 nests per 100 m²) are not rare. It should be remembered that finding the nests of the carpenter ant is not always easy, even though workers occur virtually everywhere. Therefore, the density of its nests in most biotopes is probably somewhat underestimated.

The abundance of *C. herculeanus* is decreasing towards the tree line, and at altitudes of 1000–1200 m above sea level the nests of this species are found only on south-facing slopes covered with Siberian dwarf pine. Normal nests with many adults and with brood were found on such slopes. However, the ant does not reach the upper boundary of the Siberian dwarf pine. At altitudes around 1400 m we repeatedly found single queens in chambers they had built in the soil. They probably arrived there during the reproductive flight period with ascending air, but we never found even thinly populated ("weak") nests at such altitudes.

Nests of this species in the study area, as in other parts of its range, are usually built in stumps, less often in standing dead trees and in fallen wood, and as a very rare exception, in the earth under flat stones. We have not observed

any differences in *C. herculeanus* nest organization in the Northeast of Asia from that described in the literature for other parts of its range. We should only note that in the conditions of our region carpenter ants do not penetrate the soil deeper than 5–15 cm, independently of nest position, soil type, soil water content and of the depth of the permafrost table. Most tunnels are usually built at the base of the tree trunk, and some of them perforate roots, which in the larch, as is well known, are near the surface of the substrate (Photos 35, 36). Up to 20–30 chambers (depending on the strength of the family) may be found in the roots, invariably either under bark at the lower surface of the roots or deep in the wood, within the distance of 0.5–1.5 m from the trunk. These chambers are connected by passages and serve as overwintering chambers. One of the nests excavated in winter contained 10 chambers, entirely or partly filled with ants: 4 chambers contained only workers (100 individuals in two of them, 150 and 190 in the other two), and the other 6 contained workers and larvae (100–150 workers and 100–300 larvae), in three of them, 75 winged queens and 52 males were overwintering together with workers. Some of the passages connecting the chambers also contained ants. In this nest a total of 2400 workers were overwintering, and the largest of the nests we excavated contained around 10 thousand overwintering ants.

We have observed in *C. herculeanus* a type of overwintering somewhat different from that described in the literature. In the larch forests of the floodplain terraces of the Kolyma this ant often builds overwintering chambers in decayed (easily disassembled by hands) fallen larch trees (and no other tree species!), including trunks of small diameter (10–12 cm) covered with a layer of old needles and decaying litter. In such cases the overwintering chambers are usually under bark at the lower (facing the ground) surface of the trunk or deep in its wood.

The tunnels and overwintering chambers in the nests of *C. herculeanus*, like those in the ground nests of the species described above, contained lots of large ice crystals, and ants positioned at the surface of the "overwintering ball" were partly trapped in a mass of ice crystals.

Adult ants of this species overwinter together with second and third instar larvae of small and medium size. They awaken and emerge from overwintering immediately after the snow melts. Workers bring the brood to the best-heated surface chambers, and, thus, the feeding of the larvae starts in early spring. Experiments showed that the optimal temperature for the development of this species is 27 °C (Zhigulskaya, 1987), which indicates the high temperature level suitable for the development of the eggs and larvae of the carpenter ant. Such temperatures are observed only in the upper few centimetres of soil and wood, heated by the sun, and in deeper layers the temperature is usually considerably lower.

Measurements and calculations show that in favourable years the amount of heat is sufficient for completing the development of *C. herculeanus* in one season, but in years with rainy and cool summer ontogeny cannot be completed, and larvae overwinter again. Their development resumes only next spring, but not in all the individuals: some of the second instar larvae do not develop during the second year of their life and overwinter yet another time. Experimental wintering nests contained simultaneously second, third and fourth instar larvae (Kipyatkova, 1987). Delayed development even at high temperatures (i.e. with sufficient amounts of heat) indicates the presence of endogenous diapause, similar to the diapause we demonstrated in third instar larvae of *Leptothorax acer-*

Photos 35, 36. Types of characteristic overwintering chambers of *C. herculeanus* in the roots of a larch stump. Whole families of carpenter ants never winter together in a single chamber, independently of the size of nest or roots. Diameter of pencil, used as a scale, 7 mm; diameter of root in Photo 36, 10 cm.

vorum (Kipyatkov et al., 1984). As in the species discussed above, endogenous diapause at the larval stage in *C. herculeanus* prolongs the life cycles by two or even three warm seasons and guarantees successful reproduction, and thus can be considered an adaptation to the short northern summer.

Camponotus saxatilis Ruzsky, 1885

This species is distributed from the middle reaches of the Volga eastwards, occurring everywhere in the Urals (Seima, 1971; Malozemova, 1981; Malozemova & Shvetsova, 1979), in Sibera, Yakutia (Dmitrienko & Petrenko, 1976) and in Transbaikalia (Pleshanov, 1966). It is recorded from Primorye to the Magadan Region and in Sakhalin, but not in Kamchatka. Throughout its range it lives mostly on open rocky slopes (Kupianskaya, 1990). According to M. D. Ruzsky (1905), it is a typical soil dweller. It builds a well-developed system of lengthy paths and tunnels on the surface of the earth and in the litter. Extensive excavations of the nests of this species in the Borovoye Forestry (Akmola Province, former Kokchetav Region, Kazakhstan) showed the sectional structure of nests with a horizontal system of tunnels and shafts (Malozemova, 1987). In Central Yakutia nests are sometimes found in stumps, as well as in living trees slightly burned or affected by rot (Dmitrienko & Petrenko, 1976).

In the Northeast of Asia this species was found in the Kolyma valley below (to around 50 km) and above (50–80 km) the mouth of the Korkodon on south-facing slopes covered by steppe with sparse larch trees. All the nests were in the soil and had a system of branched surface tunnels, partly running under stones.

Formica fusca Linnaeus, 1758

According to G. M. Dlussky (1967), widely distributed in the Nearctic and in the boreal Palearctic, as well as in the mountains of Central Asia and in the Caucasus. The regions of its occurrence closest to the Northeast of Asia are Central Yakutia, Buryatia, the Krasnoyarsk Territory (Dmitrienko & Petrenko, 1976) and the Baikal Region (Pleshanov, 1966). Found everywhere in diverse larch and pine forests and in cut-over areas. In the forest zone of West Siberia prefers mixed forests, pine forests, sphagnum bogs and non-floodplain meadows (Zhigulskaya, 1988; Omelchenko, 1996; Omelchenko & Zhigulskaya, 1998). Reported from the mountain forests of Tuva (Zhigulskaya, 1968) and the Altai (Omelchenko, 2004; Chesnokova & Omelchenko, 2004, 2005). Recorded in the Kuril Islands (Dlussky, 1967), Sakhalin and the northern Far East of Russia, but

absent in the Amur Region, the southern Khabarovsk Territory and Primorye (Kupianskaya, 1990). Nests in stumps, fallen trees, litter, under stones; some nests are in the earth, with small mounds. In the continental part of the North-east of Asia only a handful of nests of this species were found (Zhigulskaya, Berman, 1975; Berman, 2001). For instance, the only nest in northeastern Yaku-tia was found 30 km up from the mouth of the Nera River (right-hand tributary of the Indigirka) near the Balaganakh settlement (the species was identified by G. M. Dlussky). Near Magadan this species is not uncommon. It builds its nests in the Northeast of Asia in the same substrates as in the main part of its range.

Formica lemani Bondroit, 1917

In Europe *F. lemani* is a boreal species. In the mountains it inhabits the sub-alpine belt; in the plains of Europe it is a typical forest species; in Asia the southern boundary of its range shifts south with the plains, reaching Mongolia (Dlussky, 1967). In the Krasnoyarsk Territory and Central Yakutia *F. lemani* "... inhabits mostly mesophyte habitats in diverse types of larch forests, occurs in pine-larch forests and in cut-over areas" (Dmitrienko & Petrenko, 1976: 40). In northeastern Yakutia this *Formica* species has not been found.

This is a common species in the upper reaches of the Kolyma and in the environs of Magadan (Zhigulskaya, 1986; Zhigulskaya & Berman, 1989). The correctness of our identification of numerous collections of *F. lemani* from the Magadan Region was confirmed by G. M. Dlussky.

In the Upper Kolyma area it usually inhabits dry, well-drained south-facing slopes with deep (over 2–2.5 m) and quick thawing of the ground (Photos 37, 38). In such localities herb and herb–dwarf-shrub xerophyte and mesoxe-rophyte communities of different types are formed: relict steppes, scattered like small islands in the landscapes of the northern mountain taiga along the valleys of large rivers; meadow steppe communities (with *Pulsatilla multifida*, *Dracocephalum palmatum*, *Thymus serpyllum* and *Carex rupestris*); *Elytrigia jacu-torum* grasslands; post-fire communities (with above-mentioned plant species, saxiphrages and dog rose). Herb–dwarf-shrub sparse larch forests, as well as aspen forests with extremely thinned, often dead surface cover, also develop on such slopes. In addition, *F. lemani* was found on sand dunes of a terrace of the Linkovy Brook; the dunes, 15–20 m in height, facing the valley of the Kolyma, are not strengthened by vegetation, which forms continuous, but lax cover only in concave areas; further from the Kolyma valley, the cover increases, due, mostly, to the Siberian dwarf pine, around the bushes of which ellipses of grasses and dwarf-shrubs are formed.

Photo 37. In thinned areas, especially at outcrops of various slates, xerophyte communities are formed, completely dominated by *F. lemani*.

Photo 38. Post-fire landscape on a steep and very dry slope. Isolated bushes of Siberian dwarf pine, with typical thinned xeromorphic cover of cowberry, saxifrage (*Saxifraga oppositifolia*) and isolated clumps of sedge (*Carex pediformis*). This community is also dominated by *F. lemani*.

In the more xeromorphic steppe areas in the upper reaches of the Kolyma—near the Orotuk settlement—*F. lemani* does not occupy the main surfaces of slopes, and its nests are concentrated at forest edges. In steppe areas with a considerable share of meadow and meadow-steppe plant species (e.g. on the left bank of the Kolyma down from the mouth of the Detrin River) the density of *F. lemani* is especially high: 18–34 per 100 m². In such steppe areas nest entrances with excavated soil were found literally in each square metre of a steppe slope, the total area of which was 10–12 ha. Here we should make a reservation: accumulations of several (2–10) entrances close to each other may mark either a single nest or entrances to a single system of warming chambers lying above one of the shafts of a nest (see below). The main criterion for counting nests is the degree of spatial isolation of entrance accumulations.

The density of nests (i.e. entrance accumulations) of *F. lemani* is also high (21 per 100 m²) in thinned aspen forests, or, more precisely, thinned aspen tree stands; closed aspen forests, as any other communities, whether formed by trees or shrubs, with considerable shading of the surface or with dense surface cover, are not colonized by *F. lemani*.

In sparse herb larch forests the density of nests varies considerably. The average nest density is 8 per 100 m², and density values close to the average are typical of clearings on gentle slopes; however, in some small (20–30 m²) areas nest density reaches 70 per 100 m², and the density of entrances reaches 200 per 100 m² (Fig. 11A). On steep slopes, *F. lemani* avoids turf-free areas with unstable ground to the same degree as it avoids biotopes with closed vegetation. On sand dunes especially well strengthened by herbaceous vegetation in the valley of the Linkovy Brook we found up to 10 nests of *F. lemani* per 100 m².

In the Russian Far East this species "…forms large aggregations, colonizing remains of wood in the soil, half-decayed tree trunks and branches" (Kupianskaya, 1986b: 97). In Central Siberia its nests are built in stumps, trunks of fallen trees, under remains of wood, and, rarely, without cover (Dmitrienko & Petrenko, 1976).

In continental parts of the Northeast of Asia *F. lemani*, unlike *F. gagatoides*, builds nests with deeply positioned chambers. Its nests in this area, as we noted above, were found only in areas with deep thawing of the ground—over 2–2.5 m.

The outline of nest organization is simple (Fig. 12). In the layer of soil at a depth of 3–10 cm, under one or several stones close to each other, warming chambers are built, each of them up to 50 cm³ in size, 1.5–2 cm high. From these chambers, perpendicular to the surface, without branching, 1–4 deep (50–170 cm) shafts ending in chambers and 1–2 short tunnels (up to 20–30 cm) without chambers at the end go down. The shafts are widened, forming oval chambers (20–25 cm³), every 5–10 cm.
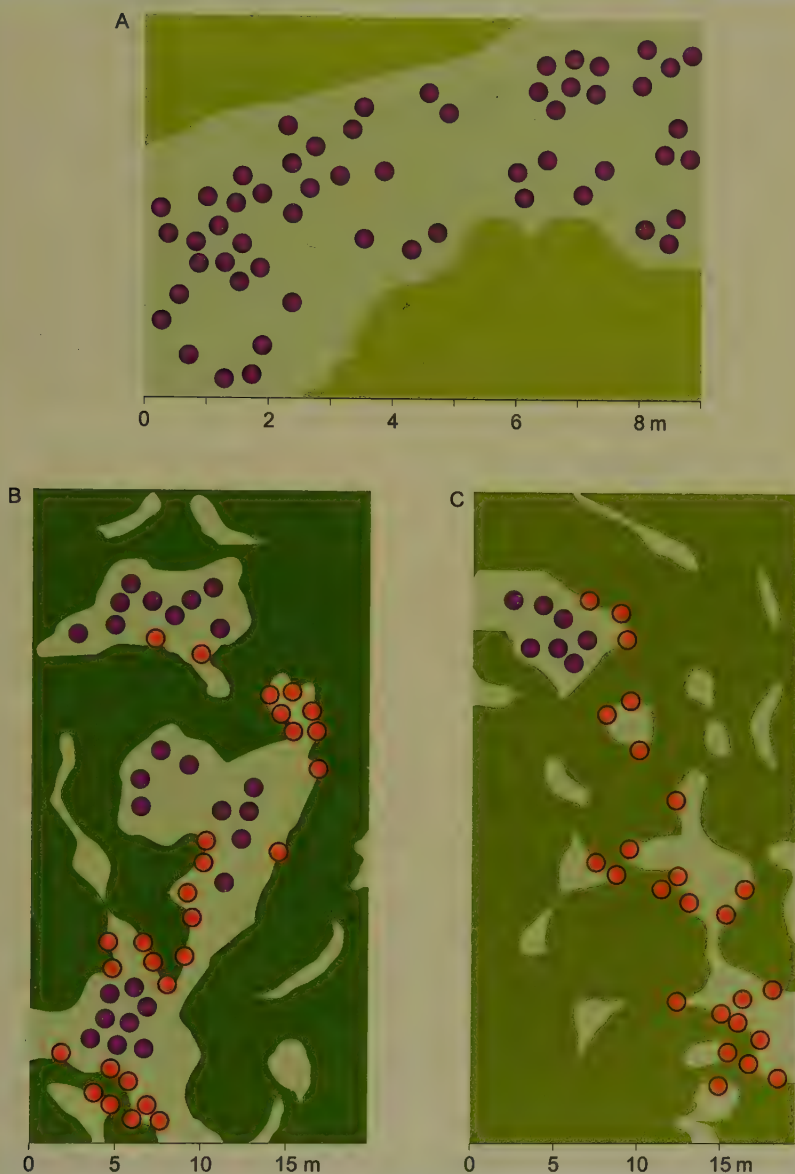
Fig. 11. Location of ant nests in habitats with different soil moisture content and degree of shading (according to mapping results). A, sparse larch forest with mesoxeromorphic herb cover and large unshaded clearings; B, mesophyte lichen–dwarf-shrub Siberian–dwarf-pine communities; clearings rather small, weakly shaded; C, herb larch forest with Siberian dwarf pine, clearings narrow, considerably shaded. Larch and dwarf pine canopy projections shaded. *F. lemani* nests, lilac circles; *F. gagatoides* nests, orange circles.

Such sectional nests may be connected by horizontal tunnels joining warming chambers ("surface horizontal system"), as well as the lower, overwintering chambers ("deep horizontal system"). The latter system is largely similar to the deep horizontal galleries in the nests of desert ants (Dlussky, 1981), although its formation in the conditions of our study area may be an adaptation to both summer and winter temperatures (see below), rather than to humidity conditions.

Nest structure may vary, depending on the locality, but the same outline is retained. Variations affect the position of warming chambers, the depth of the position of overwintering chambers and the number of sections. In nests under small flat stones, warming chambers are invariably built under the stones. In the absence of suitable stones, chambers can be built directly in the earth. Nests under remains of wood are extremely rare in continental areas: only three of the many hundreds of nests we found were under fallen trees.

On dry rubbly slopes the shafts of the overwhelming majority of the nests we excavated were running through a layer of relatively dense fine material 20–50 cm thick, usually lying at depths of 40–70 cm. The ants usually built a horizontal system of tunnels and chambers connecting the shafts along the lower surface of this layer (Fig. 12a). This system was usually the part of the nest where the ants were overwintering. Some nests had one shaft, with horizontal tunnels branching from the shaft at the depth of 60–80 cm and not connected with other tunnels (Fig. 12b).

Slopes with much fine material are densely populated, and it is possible to determine the limits of the nesting area of one family and the structure of its nest (the presence of sections, the number of short and long shafts, the number of individuals) only by complete excavation of a large area, which is, of course, extremely labour-consuming.

On rubbly and steep slopes with sparse and, usually, large families, the area occupied by a nest is more clearly visible. It is usually marked by a chain of excavated material, indicating the large chambers near the surface (no deeper than 10 cm).

The area of nests on sandy ground is clearly marked by material excavated from a number of entrances (3–10) confined to turfs of grasses and herbs, usually grouped around isolated bushes of Siberian dwarf pine (as noted above, nests are never found in areas with unstable sand). In such cases ants build only one horizontal system of tunnels, close to the surface, but rather deep, at a depth of 10–20 cm. Temperature and humidity in these tunnels are relatively high and stable over the whole summer. Shafts of such nests also go down to a depth of 170–200 cm, usually not vertically, but perpendicularly to the surface of the slope. Thus, even if the ground has sufficient humidity, the lower chambers
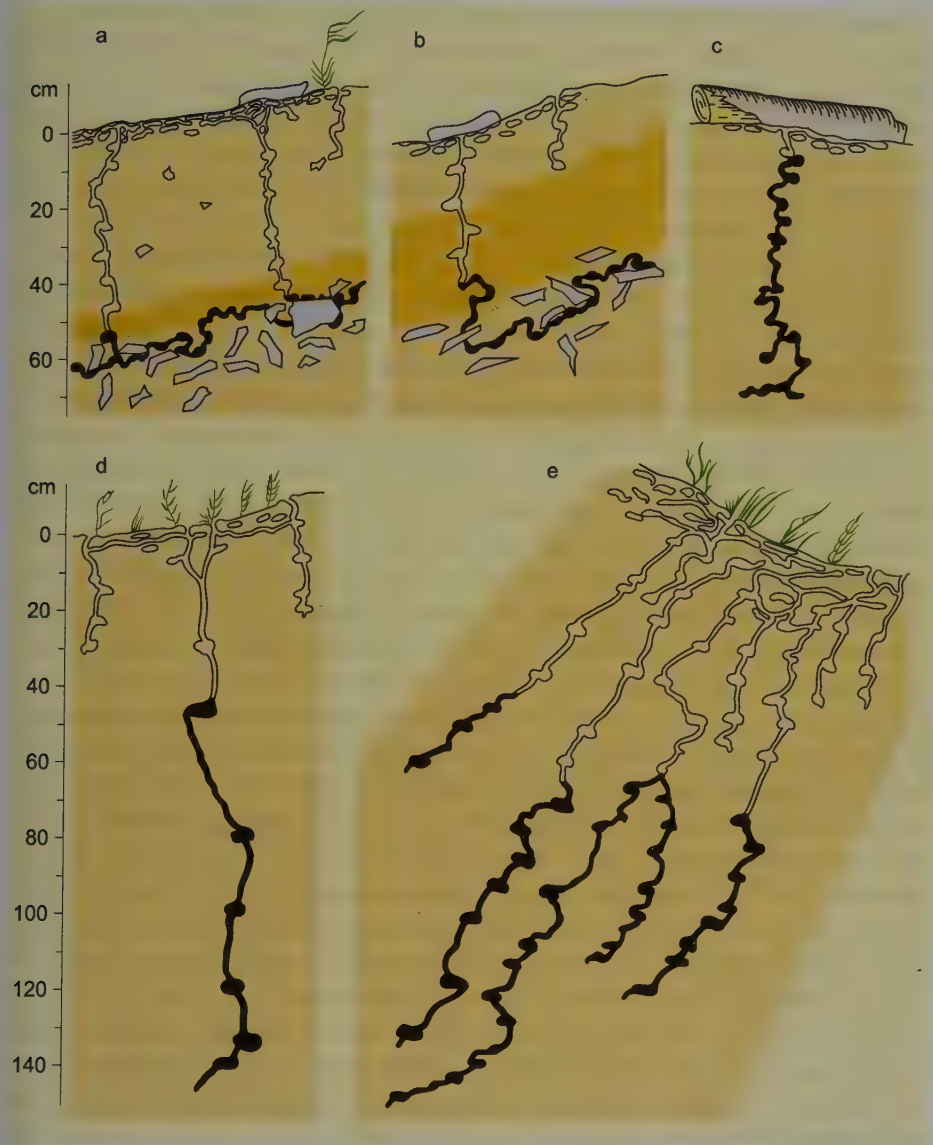
Fig. 12. Sections of *F.lemani* nests in a herb larch post-fire forest on a deluvial south-facing slope of the valley of the Olen Brook (a, b, c) and on sand-dunes in the valley of the Linkovy Brook (d, e). Overwintering chambers shown in black. For explanations, see text.

are very deeply positioned, probably reflecting the stereotypical nest-building behaviour and/or indicating an adaptation to overwintering conditions.

One of such nests, built under several small sods of grasses situated at the distance 50–70 cm from each other, excavated in late autumn, containing 330 workers and 1 female, had two shafts only 20–30 cm in length and one shaft ending at the depth 150 cm (Fig. 12d). Each of the seven oval chambers of similar size (3.5×3.5×2.0 cm) found along the entire length of the shaft, positioned one after another each 15–20 cm, contained 40–70 ants each; the lowest chamber also contained one queen.

Another, very large nest (Fig. 12e), built under a sod (70×70 cm) formed by sedge (*Carex pediformis*) and thyme, had at the depth of 10–20 cm a labyrinth of numerous large galleries (3–4 cm wide, 1–2 cm high, 30–50 cm long). The walls of the labyrinth were covered with dark dense crust of ant excretions, described in detail by G. M. Dlussky (1981) in desert ants. Four short and four deep (up to 170 cm) shafts ran down from the labyrinth, perpendicular to the surface of the slope and almost parallel to each other. The deep shafts, as well as their lower chambers, were built at a distance 10–15 cm from each other, but were not connected. It should be noted that we found no deep horizontal system of tunnels in any of the excavated nests on sandy ground.

The position of nests in extremely dry and warm localities and their architecture are clearly reminiscent of the above-mentioned similarly organized nests of desert ants (Dlussky, 1981). Our study of the microclimatic parameters of *F. lemani* habitats showed that their conditions, judging by the extreme values of these parameters, are actually close to arid. For instance, in a sparse aspen forest with isolated larch trees on a steep (around 20°) south-facing slope (600 m above sea level) the highest temperatures at the surface of bare fine material soil in the summer of 1983 and 1984 reached 62 °C (and only 34 °C in a horizontal area of moss cover). The greatest daily range of temperatures in this forest in June was 28 °C in the air (the average monthly temperature being 12.1 °C) and 46 °C at the surface of the soil, whereas the daily range of temperatures at the surface of the moss cover was no greater than 30 °C (see Fig. 9). For comparison: the highest temperature at the surface of the soil in the cold high-altitude deserts in the environs of the Pamir Biological Station was 56.8 °C, at air temperatures 20–22 °C; in the deserts of Central Asia the daily range of air temperature is no greater than 35 °C (Walter, 1975).

In the soil layer 0–5 cm deep the sum of above-zero temperatures over the hot and dry summer of 1983 was 2300 °C (at the depth of 20 this sum was 2000 °C), whereas in the air it was 1400 °C. Even at the depth of 20 cm the highest temperatures reached 25–27 °C, and the lowest temperatures over the three summer months never dropped lower than 15 °C. The temperature of the layer at the depth of 60–70 cm varied over these three months within the range of 8–10 °C, virtually without any daily pattern.

Such high temperatures, in combination with "swallow" drainage, resulted in almost complete drying-out of the soil. Humidity in the surface layer decreased to 2%; at the depth of 60 cm it was slightly higher (6%). Winter soil samples had virtually the same humidity as summer samples; however, deep horizontal systems built under the fine material horizon (see above and Fig. 12A, B) contained visible ice crystals on the lower surface of the rubble. During the next summer soil water content in the same horizons varied within the range 10–12% almost over the whole season, sometimes dropping to 4%. Deeper than 2.5 m, where the temperature is below zero all the year round, only isolated ice crystals, never strengthening the ground, indicate the presence of some humidity. This is the so-called dry permafrost (see Chapter 1); its presence, as the facts presented above make clear, has no influence on the temperatures of the higher horizons of the ground and the soil. In spring such extreme dryness results in rapid thawing of the ground, in contrast to the areas with ice-bearing permafrost, where the melting of the ice requires great amounts of heat.

It should be emphasized that it is not the water content of the soil, but rather the humidity of soil air that matters to soil-dwelling insects (Ghilarov, 1964), in contrast to plants; this humidity even in deserts is virtually always close to 100% (Rode, 1955; Dlussky, 1981). According to our measurements by loggers (autonomous computer recorders), the water vapour content of the soil air of the upper part of the profile (5–10 cm) of the most dry and warm soils of the Northeast of Asia in various types of relict steppes changed during the warm season within the range of 97–100% of saturation. Thus, soil dryness itself is not a limiting factor for the existence of ants. *F. lemani*, like desert ants (Dlussky, 1974, 1981), cannot use groundwater as a source of water. The same it true of the nests of *Leptothorax muscorum*, described above, not deep and built in extremely dry localities.

In the lower galleries of *F. lemani* nests running in horizons with sufficiently low above-zero temperatures ants possibly use the water condensing on the lower surfaces of rubble.

Somewhat different conditions are formed on sand dunes, the surface of which is heated and dried-out no less than the surface of the above-described south-facing slopes with steppe vegetation. Daily temperature ranges and the highest temperatures on these dunes are also considerable. However, the sand is always humid from the depth of 5–10 and down to the top of the permafrost at a depth of about 2.5 m. At the depth of 100 cm the temperature never drops lower than 10 °C, and at 170 cm it is never lower than 7 °C; daily pattern of temperature changes is virtually absent, as in rubbly areas.

To conclude, we would like to emphasize that all the limiting climatic factors typical of zonal landscapes of the continental Subarctic—lack of heat,

brevity of vegetation period, almost omnipresent permafrost—are at work in the Upper Kolyma basin. Their influence is smoothed out only on the dry south-facing slopes, where they are replaced by other limiting factors, typical of arid climates: excessively high temperatures and lack of humidity along the entire profile of the soil. The ability to build nests of the desert type allows the existence of *F. lemani* in biotopes unsuitable for other ants. Only in relatively softened conditions can a few other species coexist with *F. lemani*. In sparse larch forests of the south-facing slopes *F. lemani* is joined by *Myrmica angulinodis*, which occupies similar habitats, and *F. gagatoides*, which colonizes shaded localities. Both *Formica* species live side by side in such biotopes, dividing their living space approximately along the boundary of the shade thrown by larches or Siberian dwarf pines: *F. lemani* occupies open parts of clearings and *F. gagatoides* occupies areas lightly shaded by trees. The spatial distribution pattern of these species is vividly demonstrated by mapping their nests (see Fig. 11B, C).

M. angulinodis colonizes either relatively more gentle and thus less heated slopes with more humid surface layer of the soil, compared to *F. lemani*, or local depressions on the more steep slopes. In other words, this *Myrmica* species is more mesophile than *F. lemani*. Extremely rarely, and exclusively along the boundaries of steppe areas, *F. candida* is found together with *F. lemani*. In addition, the ubiquitous *Leptothorax acervorum* joins *F. lemani* where humidity is even slightly increased.

In the Sea of Okhotsk Region, probably due to the absence of permafrost in most of its mountain forest area, *F. lemani* builds its nests almost everywhere in open localities within the lower part of the forest belt (no higher than 700 m above sea level). The nests of *F. lemani* in this region, while retaining the above-described outline of organization, are less deep and may be built in wood (large fallen trees and stumps) more often than at the Kolyma. The position of *F. gagatoides* in this region, in contrast to continental areas, is inferior: on seashore it is absent not only at the edges of xeromorphic biotopes (in the upper reaches of the Kolyma it always colonizes such localities), but also in mesophyte meadow habitats, typical to this species, but in this region occupied by *F. lemani*. Although *F. gagatoides*, unlike *F. lemani*, requires only a few square decimetres for building its nest, among the 450 nests found in the course of censuses carried out along lengthy transects (over 1000 m long and 2 m wide), crossing diverse *F. lemani* habitats, and on sampling plots (10×10 m), not a single nest belonged to *F. gagatoides*: all of them were *F. lemani* nests. We believe that this situation is a consequence of the suppression of *F. gagatoides* by *F. lemani*.

In summer every nest contains workers and brood. The larvae of earlier and later instars and the pupae of workers and sexual individuals are usually grouped

in separate warming chambers; the same division into groups is sometimes observed within one chamber, but only if the chamber is large. Queens were found in every deep shaft (1–5 individuals) and almost in every short shaft (1–2 individuals). Family size, naturally, varied considerably. The results of winter excavations of several nests in a sparse larch forest on a rubbly slope of southern exposure are given below, as an example of this variation.

One of the two nests (Table 4, see Fig. 12a) had three short (20–30 cm) shafts connected to each other by surface tunnels and ending blindly, containing no overwintering ants, and two longer shafts (60–80 cm). One of the longer shafts (no. 6a) contained all the 1290 individuals found in it at a depth of 60–80 cm (three quarters of these individuals occupied a depth of 65–70 cm). Another shaft (no. 6b) contained 3400 individuals at a depth of 55–60 cm. The proportion of successful overwintering was very high: 91–98% of the ants taken from these two shafts successfully awoke at the laboratory.

The only examined shaft of nest no. 5 (see Fig. 12b) contained 4690 workers and 1 queen in chambers at a depth of 50–75 cm; the horizontal system of tun-

Table 4. Distribution of *F. lemani* ants in nests and percentage of survived overwintering individuals at different depths

Depth, cm	% of total nest population			
	Nest 1	Nest 5	Nest 6a	Nest 6b
10	20 (64*)	–	–	–
15	4	–	–	–
20	4	–	–	–
30	0.3	–	–	–
35	1.5	–	–	–
40	7.2	–	–	–
45	4.6	–	–	–
50	5.2	27 (72)	–	11
55	3	22 (83)	–	45
60	35	24	1.5	38 (91)
65	10	7	34.5	4
70	5	13 (94)	38	2
75	–	7	10	–
80	–		16 (98)	–
Total, %	100	100	100	100
Total, individuals	9007	4690	1294	3400

* In brackets, percentage of individuals awaking in the laboratory.
"–", no data.

nels branching from the shaft at the depth of 70 cm and ending blindly at the distance of 115 cm was empty. The proportion of individuals that successfully awoke at the laboratory was 94% among ants taken from the depth of 70 cm, but only 72% among ants taken from the depth of 50 cm.

The examination of nest no. 1 (Fig. 12c), which contained only one shaft, revealed the opposite, extremely rare pattern of the allocation of overwintering ants. The ants were overwintering, at depths of 5 cm and deeper, in a large chamber, containing 1800 workers, under decaying wood. The remaining 7200 ants of this nest densely filled all the tunnels and the chambers of the shaft, which went down to the depth of 70 cm and lacked any deep horizontal gallery. Two queens were found at a depth of 50 cm, and four were found at a depth of 60 cm. The impression is that this nest, the only one of the 20 nests we excavated, was for some reason unprepared for overwintering. The length of its tunnels and the total capacity of its chambers was clearly too small for such a large family, and more than a quarter of the ants had to overwinter in chambers near the surface. The survival rate of the ants taken from these chambers was lower than in normal nests, but still rather high: 64%.

Formica truncorum Fabricius, 1804

Typical of Europe (except Great Britain), all Siberia, Mongolia, mountains of Central Asia. Rare in the Crimea, the Caucasus (Dlussky, 1967) and the Baikal Region (Pleshanov, 1966). Abundant in Yakutia (Dmitrienko & Petrenko, 1976). Recorded in Primorye, the Kuril Islands and Sakhalin (Kupianskaya, 1990). In West and Central Siberia extremely rare, recorded only in the southern taiga subzone: in birch-aspen forests, in open fens and in bogs with low tree stand (Omelchenko & Zhigulskaya, 1998). In the Baikal Region this species colonizes moderately humid larch forests with an admixture of dark coniferous trees up to the altitude of 1000 m above sea level; in Yakutia it lives at the edges of pine and larch forests, in cut-over areas, at the sides of forest roads; in the Primorye it inhabits mixed and broad-leaved forests, mostly at the edges, in clearings, cut-over areas and in the bush. Nests, as in European forests, are usually built by old stumps, sometimes completely covered by the dome of the nest. Families include up to 1000 individuals (Kupianskaya, 1990).

In the continental areas of the Magadan Region this species was found only once, on the right bank of the Kolyma at the mouth of the Balygychan River in a mature herb larch forest of an old floodplain. The nest was supported by a stump; its diameter at the base was 50–60 cm.

On the coast of the Sea of Okhotsk near Magadan this species is common in larch forests. Its low-domed nests are usually built at stumps standing on south-facing slopes. A nest we excavated in the environs of Magadan had the lowest wintering chambers at the depth of 80 cm.

Formica candida F. Smith, 1878

F. candida is a widely distributed species in North and Middle Europe, Siberia, Mongolia, northern China, the Russian Far East, in the mountains of Central Asia and in Tibet (Dlussky, 1967); in East Siberia it reaches Central Yakutia (Dmitrienko & Petrenko, 1976).

In the Northeast of Asia it is common in the studied part of the Indigirka basin: from the Ust-Nera to Moma (Khonnu) villages and along the Nera River (a tributary of the Indigirka) from the upper reaches to the mouth. At the Kolyma it is found from its sources (the Ayan-Yuryakh and the Kulu) to its right-hand tributary, the Korkodon River. It will probably be found also further down the Kolyma (and its tributaries) within the forest zone in areas of floodplains with sand-and-pebble sediments. *F. candida* is also abundant in the valleys of the rivers of the Sea of Okhotsk basin (the Ola, the Arman, the Tauy etc.). It has not been found in the Anadyr basin.

This species is known for its habitat versatility. In Europe, the North and Middle Urals and northern West Siberia it colonizes peat bogs (Dlussky, 1967; Gridina, 1987); in the southern taiga subzone of West and Central Siberia (the Irtysh, the Ob and the Angara Regions) it was found only in fens and bogs and in humid mixed forests; its abundance is low everywhere: on the average 1–2 nests per 100 m² (Omelchenko & Zhigulskaya, 1998). In South Siberia it was recorded in extremely diverse habitats: in steppes, at forest edges, in wetlands, in river valleys and at high altitudes. In the mountain steppe depressions of Tuva and in the Onon–Argun steppes of Transbaikalia it lives in a wide variety of landscapes: saline (solonetz and solonchak) areas in river floodplains and lake depressions, steppe plains at the foot of mountains and steppes on mountain slopes (Zhigulskaya, 1966, 1968). In the latter type of landscapes the density of its nests is very high (usually 20–60, and up to 140 per 100 m²). Plasticity of nest-building is typical of *F. candida* in these areas (Zhigulskaya, 1969, 1975). On the northern bank of Lake Zaysan the density of its nests on steppe-meadow slopes is 2 per 100 m² (Reznikova, 1983). In the Russian Far East it inhabits meadows, broad-leaved forests and pebble areas along Thalwegs (Dlussky, 1967; Kupianskaya, 1990). In Central Yakutia it is "...characteristic of the dry types of pine, larch and pine-larch forests, steppified and steppe areas" (Dmitrienko &

Petrenko, 1976: 40), as well as of alas areas, meadows and humid larch forests; as many as 5–12 nests per 100 m² were recorded in some habitats (Dmitrienko & Petrenko, 1965). In the Baikal Region it occurs everywhere from waterlogged larch forests to dry pine-larch forests on sands, reaches up to 2000 m above sea level into the alpine belt; the density of its nests sometimes reaches 15–30 per 100 m² (Pleshanov, 1966).

In the Northeast of Asia, in contrast to South Siberia, Central Yakutia and the Russian Far East, *F. candida* inhabits only a few biotopes (Berman et al., 1981). It prefers especially the sandy-pebbly floodplains of large rivers, where it is confined mostly to forest edges and to sparse poplar-chosenia forests. It colonizes all the levels of floodplains, including the frequently flooded spits with young shoots of chosenia (Photos 39, 40, 41). It sometimes occurs also on the first above-floodplain terraces, but the exclusively also on sandy-pebbly or sandy grounds directly neighbouring the poplar-chosenia communities of high flood-plains. A peculiar feature of *F. candida*, characteristic also of *Myrmica bicolor*, is the ability to withstand long flooding of nests during high water. In years with repeated high waters in summer nests of these two species remain underwater during a total of over 1.5 months (of the 4 months when ant activity is pos-sible). In such years eggs are found in their nests only in the middle of August (Berman et al., 1981).

F. candida very rarely moves away from the floodplains, where it doubtlessly flourishes, into adjacent areas. The few cases known to us are listed below:

1) isolated nests of *F. candida* were found on a lichen-sedge-Sphagnum bog on the train of the south-facing slope of a southeastern branch of the Bolshoy Annachag Range (valley of the Olen Brook, tributary of the Sibit-Tyellakh River);

2) a colony of this species was found only once on the lower part of the slope of an ancient high sandy terrace, covered with sparse bushes of Siberian dwarf pine and washed by the Linkovy Brook (left-hand tributary of the Kolyma, lower than the mouth of the Detrin); the nests occupied a herb area (projecting cover around 40%);

3) numerous nests of *F. candida* were found on two steppe slopes: on the left bank of the Kolyma, 2 km up from the Orotuk settlement (near the mouth of the Bolshoy Tyellakh) and in the Korkodon valley. These steppe areas, judging by other groups of invertebrates and plants, are the richest in relict elements of all the steppe areas known in the Kolyma basin. Though the nests are positioned in narrow erosional depressions with meadow vegetation and isolated larch trees, the ants hunt in steppe communities: during morning hours of sunny days we recorded up to 20 foraging workers per m². It should be noted that *F. gagatoides*, which in the absence of *F. candida* always colonizes such depres-

Photo 39. In such loose sandy-pebbly substrates *F. candida* and *M. bicolor* build their nests. In the foreground, numerous entrances, renovated after flooding, to a nest of *F. candida*.

Photo 40. Close-up of the same nest (cigarette lighter is used as a scale).

Photo 41. In some years, nests of *F. candida* and *M. bicolor* remain without detriment under ice-cold water for over a month. The photo shows spring flood on the Arman River.

sions bordering steppe areas, does not go into steppe communities for foraging. In many other examined steppe areas in the Kolyma valley *F. candida* was not found, probably because steppe slopes, except the above-described, are supported not by sandy-pebbly floodplains, but by waterlogged above-floodplain terraces where this species is missing. It is unclear why *F. candida* is absent on the steppe slopes at the Indigirka, since this species is abundant in floodplains adjacent to these slopes, and the high temperatures of steppe areas, judging by the habitats of this species in the mountain steppes of southern Siberia, are unlikely to limit its distribution.

All the nests of *F. candida* found in the Northeast of Asia are built entirely in the ground (Fig. 13), without using any remains of wood or building any surface structures, as in nests found in Tuva (Zhigulskaya, 1975), Yakutia (Dmitrienko & Petrenko, 1976) and the Baikal Region (Pleshanov, 1966). Materials excavated from these nests built ("hillocks") are no larger than 10 cm in diameter and 1–2 cm high; the nests usually form groups of 5–10 occupying the area of 10–15 m^2. Nests within each group are connected by a network of underground tunnels perforating the upper 5 cm of the soil. The groups are connected by sparser tunnels; such colonies often occupy areas of up to 0.5 ha. Deep shafts go from the centre of each group down to depths of 30–50 cm, where they end in 2–3 chambers 7–10 cm^3 in size. Warming chambers for brood, up to 25 cm^3
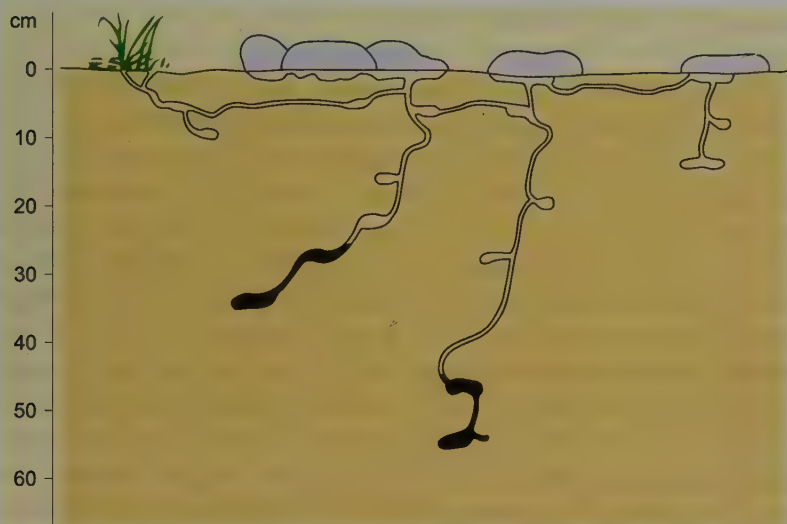
Fig. 13. Section of a *F. candida* nest on a low sandy-pebbly spit. Stones are shown in gray. Overwintering chambers shown in black.

in size, are built either under stones or near the surface of the soil. In sandy grounds warming chambers are built in tangles of roots strengthening the sand.

The nests of *F. candida* in a sphagnum bog were built in large (up to 1.5 m in diameter and 40–60 cm high) and lax sphagnum "pillows" overgrown with stunted cowberry, bog-rosemary etc. The surface of the "pillows" was partly covered with a 3–5 cm layer of excavated moss, in which numerous warming chambers were built. The deep part of the tussock was also perforated by tunnels, which did not go out of the tussock because of the excessive humidity of the area between tussocks. Nests were removed from each other to distances greater than 1 m, and no tunnels connecting them were found.

The overwintering ants are adult workers and wingless queens. Only one winged queen was found in all the nests excavated over several winters; this queen successfully survived overwintering (awoke in laboratory conditions). Worker ants were overwintering together with queens in chambers at depths of 30–50 cm; the upper chambers contained few individuals, whereas the deeper chambers contained several hundreds of them. A total of up to 500 individuals were found overwintering together in the deeper chambers.

Thus, in the Northeast of Asia *F. candida* displays habitat versatility, retaining its ability to exist in various biotopes, but actually prefers only unshaded areas of floodplains with sandy-pebbly ground.

Formica gagatoides Ruzsky, 1904

F. gagatoides is the only Palaearctic species of ant not found in the plains south of 60° N. In mountains it goes far into the south. It was found in the Pod-kamennaya (Stony) Tunguska basin (Dmitrienko & Petrenko, 1976), in the Middle Urals between 58° and 59° N (Gridina, 1987) and in the Sikhote-Alin (Kupianskaya, 1990); one isolated population is known from the mountains of central Japan at 35–36° N (Sonobe & Dlussky, 1977). It is definitely absent in the southern taiga of West Siberia and the Angara Region (Omelchenko, 1996; Omelchenko & Zhigulskaya, 1998). We believe that it can be found at medium altitudes throughout the area from the basins of the Kolyma and the Indigirka (see below) to the mountains bordering the basin of the Amur's left bank.

F. gagatoides is undoubtedly the northernmost *Formica* species; however, its range does not reach into true tundras (Dlussky, 1967). In spite of careful search, this species was found neither in the mountain tundra parts of the basins of the Amguema and the Bolshaya Osinovaya nor in shrub communities of the Chaun Bay coastal areas and of the lower reaches of the Kolyma (typical tundra sub-zone). The northern boundary of its range, judging by fragmentary observations in different localities of the Northeast of Asia, coincides with the boundary of the continuous range of the Siberian dwarf pine, whereas in dwarf-pine forest-tundras (thinned dwarf pine communities at the border between tundra and forest tundra) this species is absent.

In forest and mountain forest areas of northeastern Yakutia and the Magadan Region *F. gagatoides* is among the most abundant species, together with *Leptothorax acervorum* and *Camponotus herculeanus*. It occurs below the tree line (900–1000 m) almost everywhere except in extremely dry, overwet-ting and strongly shaded localities, such as relict steppe areas, dense forests or yerniks, and sedge wetlands; however, it readily colonizes moss bogs. The highest density of its nests, 40 per 100 m², was observed in well-drained (standing on washed-out moraine boulder beds) herb–dwarf-shrub larch forests. Such nest density and average family size of 500 individuals (not counting the brood; see below) make *F. gagatoides* a dominant species of the soil and soil surface com-munity (not counting dendrobionts), representing more than half of the total abundance (424 specimens per m²) and biomass (1.9 g per m²) of all the soil macrofauna arthropods of this community (Berman & Bukhkalo, 1985).

Nest density is considerable (10–20 per 100 m²) also in thinned dwarf-shrub–moss larch forests with uneven nanorelief, in dwarf-shrub–lichen sparse larch forests, in cut-over areas in herb–dwarf-shrub larch forests, in thinned Siberian dwarf pine bush on sandy loam soils etc. All these habitats attract ants not only by strong illumination and moderate humidity of the upper part

of the soil profile, but also by fallen trees, often used by ants for building the aboveground part of their nests. *F. gagatoides* nests are sparse (1–2 per 100 m²) in localities not fulfilling these requirements (or one of them).

In mountain tundras isolated nests of *F. gagatoides* occur up to the altitude of 1200 m above sea level, but only on south-facing slopes, and the abundance of this species dramatically declines, due to the decreasing heat supply, at altitudes of 900–1000 m (Berman et al., 1980).

In the Northeast of Asia *F. gagatoides* builds its nests, as in East Siberia (Dmitrienko & Petrenko, 1976), without cover in the soil, under flat stones, in standing dead trees, stumps, fallen trees, wood remains and moss "pillows"; very rarely its nests have a small (up to 20 cm in height and diameter, as if unfinished) piled-up dome made of plant debris, as in nests of *F. exsecta* (Fig. 14). Sometimes nests of mixed type are found: ants pile up "pads" of small plant debris either by a stone or a fallen tree, under which they build their warming chambers. In stumps, fallen trees and standing dead trees warming chambers are built under bark, whereas overwintering chambers are always built in the soil or in half-decayed roots at the depth of 10–20 cm. In old large fallen trees and stumps (rotten or "processed" by *Camponotus herculeanus*) tunnels of *F. gagatoides* go into the wood. It should be noted that *F. gagatoides*, like other ant species, uses for building its nests (or only warming chambers) mostly remains of larch wood and, extremely rarely, of Siberian dwarf pine wood, ignoring all the other tree species. Nests under stones have large warming chambers, usually with a single shaft going down and ending in overwintering chambers at depths of 15–20 cm, less often 30 cm. In summer these chambers can be flooded with groundwater, but ants occupy them again after the level of the water decreases. Sometimes one family builds its warming chambers under several stones lying close to each other. The underground tunnels of such nests communicate in the layer 10–15 cm deep, and the overwintering chambers are built, as usual, at depths of 15–30 cm.

Nests in sphagnum "pillows" have the following organization: two or three tunnels, almost not branching and seldom connecting, but lengthy, are built directly under the surface; these tunnels are widened, mostly at the top and on the southern side of the pillow, forming a few warming chambers. Such surface tunnels gradually go deeper into the pillow (to the depth of 20–30 cm), where they end in two or three oblong chambers, positioned one after another at a distance of 5–7 cm; the size of each of these chambers is 9–10 cm³. According to V. K. Dmitrienko and E. S. Petrenko (1976), nests of *F. gagatoides* built in moss tussocks are characteristic of the northern boundary of its range. Such nests were found neither in Central Yakutia nor further south.

In spite of all the diversity of its nests (Berman et al., 1987a), *F. gagatoides* never builds branching networks of tunnels and chambers characteristic of the
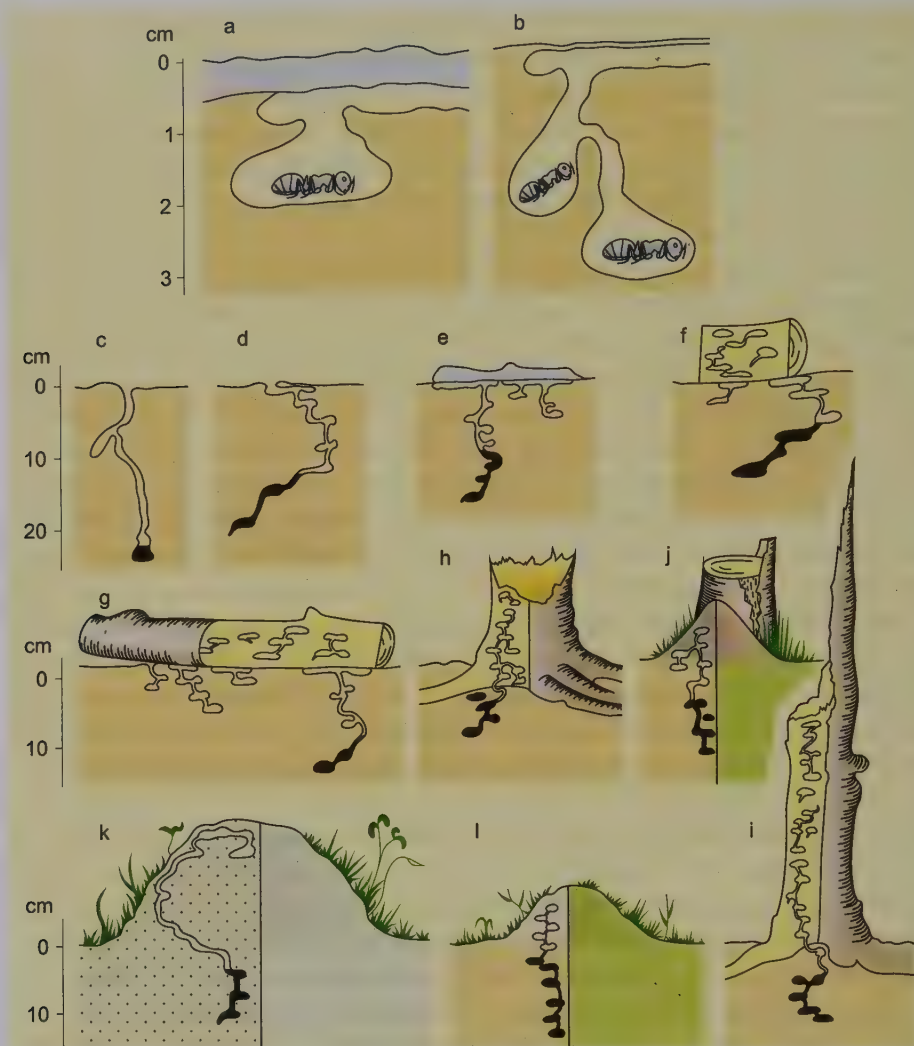
Fig. 14. Nests of *F. gagatoides* in the Upper Kolyma region. Young nests: with one (a) and two (b) females; with one female and eight workers (c). Completely formed nests: without any cover (d); under stones or fallen trees, in stumps or dead wood (e, f, g, h, i); in a stump with soil "pad" (j); in sphagnum tussocks (k); with cone of plant remains (l). Overwintering chambers are shown in black.

ground nests of many other ant species (Dlussky, 1981), and invariably built by *F. lemani* in our study area (Zhigulskaya, 1986).

The aboveground structure of the nest depends on habitat type. In strongly illuminated localities warming chambers are built in the surface layer of the soil

above overwintering chambers, and any aboveground part is absent. In mountain tundra nests are built only under stones. In sparse forests diverse materials are used as cover. In areas with a dense herbaceous layer and few potential covers, as well as on northern slopes, warming chambers are sometimes built at some distance from overwintering chambers, and in standing dead trees we found warming chambers under bark even as high as 60–100 cm above the ground; on sunny days almost the entire family gathers in these chambers.

While the organization of the aboveground part of the nest varies considerably, its underground part is relatively constant: overwintering chambers are of the same type and never built deep in the earth, both in well-drained areas with a thick seasonally thawed layer and in wet areas with permafrost lying close to the surface. Tunnels built on sandy soils, thawing quickly and deeply and, thus, allowing insects to emerge early in spring, also never go deeper than 30 cm, though in two other species inhabiting the same localities (*F. exsecta* and *F. lemani*) overwintering chambers are positioned very deeply, at 100–200 cm. Therefore, the surface position of the tunnels and chambers of *F. gagatoides* can be viewed as a result of its stereotypical behaviour, which frees this species from dependence on permafrost. Although the chambers of *F. gagatoides* are built deeper than in *Leptothorax acervorum*, *L. muscorum* and *Camponotus herculeanus*, it lives so close to the surface of the soil that it is apparently not affected by permafrost. Neither the high position of the impermeable ice-bearing permafrost table nor the cooling effect permafrost has on the soil prevents *F. gagatoides* from nest-building, and, thus, permafrost almost never limits the habitat distribution of this species. The only exceptions are areas with very high level of groundwater or of permafrost table, e.g. some communities with moss cover. Lengthy and deeper tunnels of *F. gagatoides* help this species to colonize biotopes with a strongly dried-out surface horizon of the soil, unsuitable for *L. acervorum*. This feature of the tunnels of *F. gagatoides* also determines the subordinate role played in its nests by nanorelief exposure: ants of this species are probably capable of finding currently suitable conditions by moving together with their brood between parts of the tussock of different exposure.

The landscape and habitat distribution of *F. gagatoides* is largely similar to that of *L. acervorum*, and in most cases these two species occur together. The differences observed between them are largely determined by their different body and family size. *L. acervorum* requires limited living space: a few dozen square centimetres are sufficient to accommodate a nest of this species. The ease with which *L. acervorum* can find tiny spaces with quite specific conditions against any, even unfavourable, background, is, as shown above, one of the reasons for the wide distribution and high abundance of this species.

F. gagatoides has a greater nest and family size, and, naturally, requires both larger spaces for building its nests and larger hunting territories (probably many square metres).

These differences between the two species result in certain shifts in their patterns of habitat distribution: *L. acervorum* is most abundant in localities with well-drained, but not dried-out surface horizon, whereas *F. gagatoides* is relatively indifferent to surface soil layer humidity, but intolerant of the drying-out of the horizon 20–30 cm deep.

Winter family composition in *F. gagatoides*, as in all the other *Formica* species studied in the region, is always the same, since only workers and wingless queens overwinter. One of the nests excavated in winter (Table 5) contained 808 workers and 3 queens, overwintering in six chambers at depths of 6–17 cm (three chambers with 58, 68 and 145 workers at 6 cm, one chamber with 122 workers at 10 cm, one chamber with 194 workers and 1 queen at 12 cm, and one chamber with 231 workers and 2 queens at 17 cm). The other families contained from 180 to 790 individuals, including 1–3 queens, overwintering in 3–5 chambers at depths of 5–25 cm. Nests chambers of single queens were positioned no deeper than 7 cm, and a young nest with 1 queen and 8 workers was built at a depth of 22 cm.

We found individuals of *F. gagatoides* also as "slaves" in nests of other species. One nest (no. 8, Table 5) contained 246 workers of *F. gagatoides* and 277 workers of *F. sanguinea* overwintering together; another (no. 7, Table 5) contained 190 workers of *F. gagatoides* and 600 workers and 1 queen of *F. exsecta*, and yet

Table 5. Family structure and depth of chamber position in *F. gagatoides* in winter

Nest no.	Date of excavation	Depth of overwintering chambers, cm	Number of overwintering chambers	Family composition (individuals)	
				workers	females
1	16.X.1976	10–12	1	198	2
2	18.I.1978	8–12	4	590	3
3	6.II.1979	17–22	4	370	no data
4	25.IV.1980	12–20	3	180	3
5	25.IV.1980	10–21	3	358	2
6*	23.III.1983	3–30	20	4500	no data
7	26.III.1984	14–21	10	790	3
8	10.X.1984	10–23	7	523	1
9	26.III.1984	5–7	3	545	2
10	29.III.1985	6–17	6	808	3
11	31.III.1985	6–13	4	740	3

* In nests nos. 6, 7, 8 ants of this species lived as "slaves" of other species (for explanation, see text).

another (no. 6, Table 5) contained 1500 workers of *F. gagatoides* and 3000 work-
ers of *F. sanguinea*. We are not discussing in this essay the relationship of the
latter two species, but it should be noted that sexual individuals of all *Formica*
species emerge in nests in large numbers during the last ten days of July, and
in years with cold summer many of them were recorded in some nests even in
September. During the days of reproductive flight, in areas with high density of
F. exsecta nests, almost every nest of *F. gagatoides* contained queens of *F. exsecta*
that had already finished their flight but had not yet shed their wings.

Three of the 11 excavated nests contained myrmecophilous rove beetles
Lomechusoides pr. *inflatus*[1] (Zetterstedt, 1928), (Staphylinidae, Coleoptera): two
nests with 3 beetles each and one nest with 9 beetles.

Overwintering individuals are always found in deep chambers, lying in close
contact with each other. Tunnels, as in other species, contain ice crystals. Usually
300–500 workers (at most 1000) overwinter in one nest with 2–3 queens. Some
of the nests we excavated in winter contained many winged females, which suc-
cessfully overwintered, as was shown by their awaking in the laboratory.

Formica sanguinea Latreille, 1798

A widely distributed Palaearctic species. Its range includes Europe, central and
southern European Russia, the Caucasus, South Siberia to the Ussuri Region,
Japan, northern Mongolia, the Tien Shan, Tibet (Dlussky, 1967) and Central
Yakutia (Dmitrienko & Petrenko, 1976). In the forests of Europe it prefers open
areas and meadows (Dlussky, 1967). In West Siberia it typically occurs in forest-
steppes (Reznikova, 1983) and is rare in the forest zone. In the southern taiga
subzone of West and Central Siberia it is recorded in cut-over areas, bogs and
birch-aspen forests (Omelchenko & Zhigulskaya, 1997, 1998), with extremely
low nest density (less than 0.1 per 100 m²). In the middle and northern taiga of
these regions it has not been found (Omelchenko & Zhigulskaya, 1981). It was
found in Yakutia in larch forests and cut-over areas (Dmitrienko & Petrenko,
1976), in the Angara Region in birch-aspen forests and cut-over areas (Zhig-
ulskaya, Omelchenko, 1977), in the Baikal Region everywhere in larch and pine
forests and steppe (Pleshanov, 1966) and in Tuva only in floodplain forests and
saline meadows (Zhigulskaya, 1969). In the Primorye, the Khabarovsk Territory,
Sakhalin and the Kuril Islands it occurs in forest clearings (Kupianskaya, 1990).
Generally, in most of its range this species preferably occupies open biotopes,
and in forests it prefers thinned types of them, as well as clearings, forest edges,

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[1] Identified by A. S. Ryabukhin.

cut-over areas etc. It nests in stumps, fallen trees, less often in the soil or under stones. The aboveground structures of its nests are small mounds of twigs, needles and dry litter. Its wintering shafts sometimes go down as deep as 1 m. Nests contain up to 20 thousand individuals (Kupianskaya, 1990).

In the Upper Kolyma area the nests of *F. sanguinea* are also found in moderately humid sparse larch forests (at altitudes up to 800 m above sea level). This species is clearly suppressed at the Upper Kolyma, compared to other parts of its range, which is indicated by the sparse occurrence of its nests and their small size, in spite of the abundance of the nests of potential "slaves". Most nests are isolated. We found only one nest group, some 20 nests occupying an area of around 3 ha, no closer than 20 m from each other. All the *F. sanguinea* nests that we found were either by stumps or by fallen trees and had piled-up mounds or "pads" of plant debris, similar to the nests of *F. gagatoides* or the younger nests of *F. exsecta*.

We have not found any division into summer and winter nests, recorded in Europe, never observed migrations from one nest to another and found no nests without "slaves" (Dlussky, 1967). The absence of nests without slaves is probably explained by the abundance of *F. gagatoides* in the habitats occupied by *F. sanguinea*, and, thus, by the availability of *F. gagatoides* pupae. Only workers of *F. gagatoides* were found as "slaves" of *F. sanguinea* in the Upper Kolyma, reflecting the separation of the habitats of *F. sanguinea* and *F. lemani* and the extreme rarity of *F. fusca* in this area.

The results of the excavation (15 July 1983) of a medium-sized nest, built at the southern side of an almost undestroyed stump (20 cm in diameter) give the idea of the family composition of this species. This nest had a "pad" in the shape of a mound 15 cm high and 35 cm in diameter at the base. The upper part of the nest was rather densely perforated with tunnels and chambers, and only 3–4 shafts went down, running along the roots of the stump and forming several widenings, or chambers (the entire family overwinters in such chambers at depths of 20–30 cm). The nest contained 206 workers of *F. sanguinea* and 313 workers of *F. gagatoides*. They were found both in the mound and in the deepest chambers. A queen *F. gagatoides* was found at a depth of 10 cm together with 15 workers of *F. sanguinea* and 40 workers of *F. gagatoides*, as well as 120 pre-pupae and 420 pupae. The pupae included 180 workers and 90 males of *F. sanguinea* and 150 workers of *F. gagatoides*; the nest already contained no eggs or larvae.

Formica exsecta Nylander, 1846

F. exsecta is a Palaearctic boreal species, with the northern boundary of its range running north of the Arctic Circle in Europe, across the lower reaches of the Ob

in West Siberia (Dlussky, 1967) and along the 60th latitude in Central Siberia (Dmitrienko & Petrenko, 1976). The southern boundary of its range coincides approximately with the southern boundary of the forest-steppe zone and runs across the Altai, Tuva, Transbaikalia, northern Mongolia, the Ussuri Region and Japan. In South Europe this species was recorded in the Alps and in the Balkan Mountains (Dlussky, 1967). In West and Central Siberia it is rare (at most 0.5 nests per 100 m²), and in southern taiga occupies open fens and small woods (Omelchenko & Zhigulskaya, 1998). In the Baikal Region it is extremely rare (Pleshanov, 1966). In Central Yakutia and the Angara Region it is confined to larch, pine and birch forests, where the density of its nests is also low, at most 1 per 100 m² (Dmitrienko & Petrenko, 1976). The reported findings of this species in Primorye (Kuznetsov-Ugamsky, 1928; Dlussky, 1967), according to A. N. Kupianskaya (1990), refer to *Formica rufomoculata* and *F. longiceps*. It is also known from the Khabarovsk Territory and Kamchatka (Kupianskaya, 1990), where it is common at forest edges, in clearings of larch forests and in cut-over areas. Its nests usually have a piled-up conical dome of plant debris and needles with diameter at the base up to 100 cm and height up to 40 cm; the largest anthills reach 200 cm in diameter and 70 cm in height.

In the Northeast of Asia *F. exsecta* is regularly found in the forests of the Sea of Okhotsk coast and in the Upper Kolyma basin (Photos 42, 43). This species has not been found lower than Zyryanka village, but it is quite probably also present along the middle reaches of the Kolyma, especially on its right bank, as well as at the Omolon and the Anyuy. It was found at the Anadyr in the environs of Markovo village in clearings in a larch-poplar-chosenia forest; in the adjacent tundra and mountain tundra landscapes it is absent (Berman et al., 1980, 1984). At the Indigirka, in spite of careful search, this species was not found in any of the examined localities (Zhigulskaya, 1976); however, it is common by the Lena south of Yakutsk (Dmitrienko & Petrenko, 1976).

In the main part of its range *F. exsecta* occupies a wide scope of landscapes, with a preference for thinned forests, clearings, forest edges, cut-over areas etc., and in the south it shifts towards either the tree line (Atanassov, 1952), or forest edges on northern slopes (Zhigulskaya, 1969). In the Northeast of Asia it retains its preference for thinned forests, but avoids the slopes of northern exposure.

In the sparse forest belts at altitudes up to 500 m nests of *F. exsecta* were found in four habitats: on a sandy terrace of the Kolyma, covered with lichen dwarf-pine communities; on levees of the Kolyma with herb larch forests; in some areas of the terraces of the brooks Ozyorny and Olen (tributaries of the Sibit-Tyellakh River), occupied by moderately humid larch forests with large willows; and in a moss–dwarf-shrub sparse larch forest on a train of a south-facing slope. Most of the nests are isolated, only rarely they form colonies of 25–35.
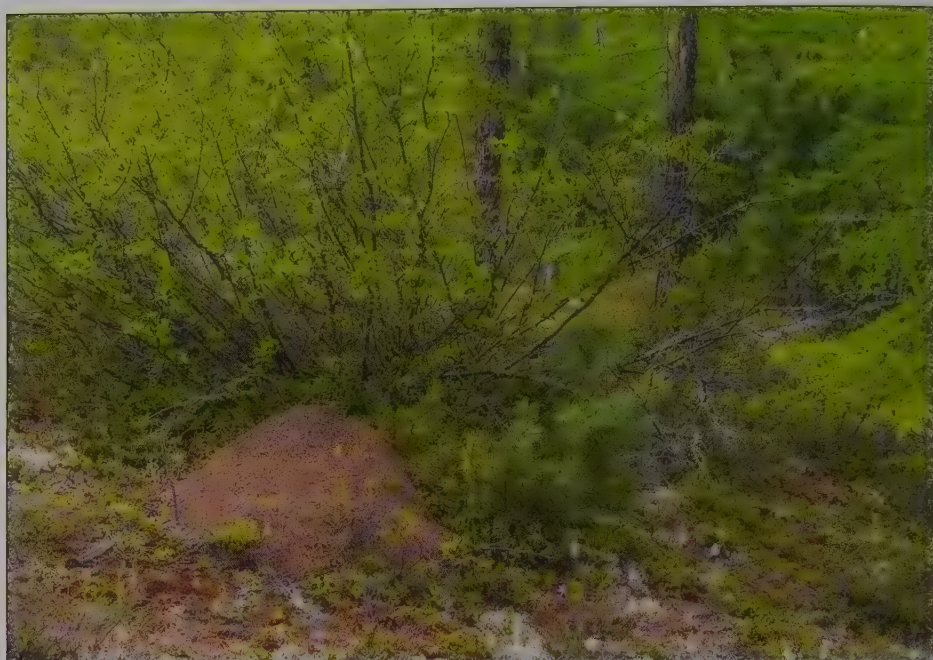
Photos 42, 43. Typical nests of *F. exsecta* (diameter at base 35-40 cm) in the Upper Kolyma area.

In the valleys of the Olen, the Sibit-Tyellakh and other examined basins nests of *F. exsecta* were found at altitudes from 500 to 800 m above sea level only twice: a small colony (10–15 nests) in an erosional depression with gentle slopes, covered with a moss–dwarf-shrub larch forest, and isolated nests in another shallow erosional depression, in a herb-cowberry larch forest with Siberian dwarf pine. At altitudes higher than 800 m (up to 1200 m above sea level) *F. exsecta* was occasionally found in isolated nests only on slopes of southern exposure. More surprising was our finding of this species in huge numbers in the depression of Jack London Lake, adjacent to the Sibit-Tyellakh basin, at altitudes of 800–1000 m above sea level. Although the bottom of this depression is close to the tree line, it is dominated by sparse larch forests and dwarf-pine communities, and not by mountain tundras, due to the well-drained moraine sediments and the absence of strong winter winds. The watershed between the Sibit-Tyellakh River and Jack London Lake is almost imperceptible in the relief (900 m above sea level); the vegetation on both sides of the watershed also shows no differences. However, immediately after crossing the watershed the nests of *F. exsecta* are found in great numbers. In the Sibit-Tyellakh basin *F. exsecta* generally occurs locally, whereas in the depression of Jack London Lake it occupies a wide variety of habitats (Table 6): from diverse types of moderately humid larch forests and dwarf-pine communities to tussocky cotton-grass–sedge waterlogged sparse larch forests in brook floodplains. The density of its nests is sometimes high even across large areas (usually up to 40–47 nest per km of a census route), and the gaps between its colonies are never wider than 100–300 m. The number of nests in the densest colonies reaches 12 per 100 m². It is much easier to list the biotopes where *F. exsecta* is absent in this depression than those where it is present. It does not occur on steep northern slopes of moraine ridges and sides of the depression; and in the beds of melted aufeis fields; on very dry rubbly crests of ridges, covered with Siberian dwarf pines and isolated larch trees. Nests of this species are also absent in overwetting or waterlogged larch forests, dwarf-shrub–sphagnum, without distinct tussocky microrelief, or tussocky, of different type, with constantly high (higher than tussock bases) water level, and in closed dwarf-pine and alder communities.

The appearance of *F. exsecta* nests is extremely variable, depending on their position. Domes are broad at the base and flattened in dry areas with thinned tree stand (Fig. 15A-I) and almost perfectly conical in slightly shaded areas (Fig. 15A-II). If the nest was initially built in a tussock on sedge wetland, the cone of its dome is always high and broad at the base (Fig. 15C-I); if the nest is shaded or built among sedges, the height of the cone is the same, but its base is usually narrow (Fig. 15C-II). The cone is in most cases asymmetrical: its southern side is gentle, whereas its northern side is almost vertical. In cotton-grass–

Table 6. Density of *F. exsecta* nests in principal plant communities of the depression of Jack London Lake (per 100 m of transect 20 m wide)

Vegetation and humidity	Length of transects, m	Number of nests	
		average	extremes
Sparse larch forests			
Siberian-dwarf-pine–lichen (dry)*	1100	4.7	1–9
Siberian-dwarf-pine–moss (wet)	1200	2.8	1–6
Siberian-dwarf-pine–large-shrub (wet)	2700	2.1	0–3
shrub–lichen (dry)	1300	4.5	1–9
subshrub–green-moss (wet)	1300	3.3	1–12
subshrub-sphagnum (damp)	5100	4.5	1–9
tussocky moss–sedge–cotton-grass (damp)	1100	4.0	1–8
lichen (dry)	1200	2.1	1–4
Siberian-dwarf-pine–lichen (very dry)	7200	0	–
dwarf-shrub-sphagnum (overwetting)	2500	0	–
tussocky moss–sedge–cotton-grass (with water windows)	1700	0	–
tussocky sedge-subshrub (with watercourses)	2000	0	–
Siberian dwarf pine communities			
various types, very dry	1200	0	–
closed (wet)	2500	0	–
Riverbank yerniks (including bottoms of aufeis fields)	5200	0	–
Floodplain meadows	700	0	–

* From cenotic point of view, various sparse larch forests with Siberian dwarf pine are communities of the dwarf pine rather than of the larch.

sedge tussocky larch forests the domes of *F. exsecta* are sometimes also built on tussocks (Fig. 15C-I), and old nests become mushroom-shaped, because the peripheral part of the dome overhangs the sides of the tussock, being 15–20 cm broader than the tussock, with sides supported by living and dry sedges (see also Chapters 3 and 5). The structure of nests built in sphagnum larch forests with their typical smoothed tussocky microrelief ("pillows") is transitional (Fig. 15B). The material of the cone also varies: in sparse larch forests the dome is built almost entirely of small pieces of *Cladonia* and *Alectoria* lichens, which determine its unusual light green colouration. Materials collected by ants in post-fire ecosystems consist mostly of burned twigs, which make the domes almost black; the domes built under the canopy of larch trees can be straw-coloured because of dry needles, of which almost the entire dome is often built.

Nest size is usually small. Of the 150 nests recorded along a route crossing the main plant communities of the Jack London Lake depression, 41 (27.3%) were around 60 cm in diameter at the base of the dome (Table 7). Only one
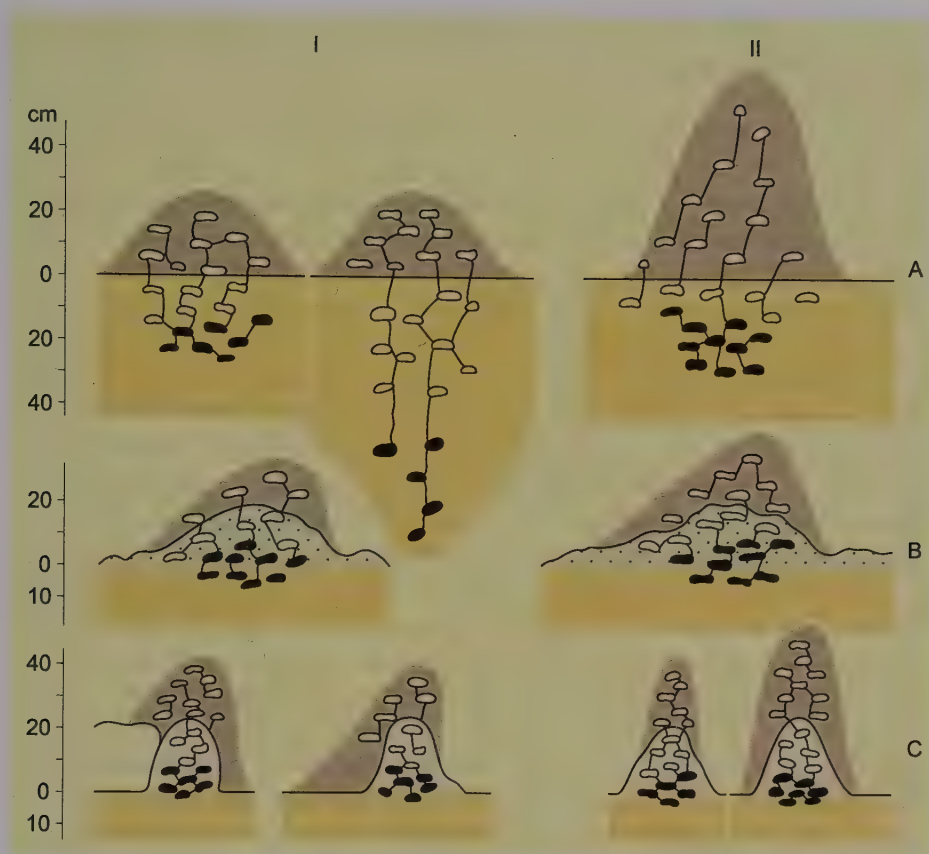
Fig. 15. Cone structure and distribution of overwintering chambers in nests of *F. exsecta* in localities with different soil moisture content (A, B, C) and degree of shading (I, II). A, sand bank of the Kolyma River, moderately damp; B, wet tussocky sphagnum larch forests; C, tussocky sedge wetlands. I, open areas; II, under forest canopy. Oblique hatching is the piled-up part of the cone consisting of plant remains. Overwintering chambers are shown in black.

Table 7. Size of *F. exsecta* nests (n = 150)

Diameter of dome base, cm	Proportion of all nests found, %
less than 20	19.5
21–40	29.3
41–60	36.0
61–80	14.6
120	0.6

nest was twice as large (120 cm in diameter, 70 cm high). Nests built on tussocks reached 140 cm in height (80 cm the tussock and 60 cm the cone) and 60 cm in diameter.

Nests of *F. exsecta* in the Northeast of Asia are distinguished from those described in central parts of its range (Dlussky, 1967) by the surface position of their underground structures. Typical nests of the ants of this group have lower chambers at depths of 100–120 cm (Dlussky, 1967), whereas the lowest chambers found in any of the 29 nests we excavated at the Kolyma were barely reaching the depth of 40 cm, and usually their tunnels did not go deeper than 20–30 cm from the surface of the soil. The tunnels and chambers of nests built on sedge tussocks never lay deeper than the base of domes (Fig. 15C). There are two reasons for the surface position of the chambers and tunnels in the Northeast of Asia. In most habitats the depth of soil tunnels is limited by the summer level of groundwater, which marks the position of the lowest chambers. By autumn ants move deeper, with decreasing level of groundwater, which is caused, above all, by the increasing thickness of the seasonally thawed layer and, thus, the depth of ice-bearing permafrost table. Consequently, the soil layer insulating ants from decreasing air temperatures becomes thicker. In those habitats where winter temperatures are already high enough at 20–30 cm from the surface, ants do not go deep into the soil for overwintering, even though the depth of their overwintering is not limited by the level of groundwater (see below). Such situations are observed, for instance, in mountain tundras of south-facing slopes. The high position of the overwintering chambers is especially advantageous in spring, since it provides early heating and, thus, early awaking of ants and prolongs the period of their seasonal activity.

The only, but fundamental, exception to this rule were the nests found on sandy terraces and levees of the Kolyma, with overwintering chambers at depths of 120–130 and 40–60 cm, respectively (Fig. 15A). In winter, due to low groundwater levels, ants of in these habitats can escape the low temperatures of surface horizons and awake in spring without delay, since dry ground thaws quickly and deeply.

In the course of winter excavations ants were found in overwintering chambers in the "walking" position. The total number of individuals overwintering in different nests was from 1200 to 5800, with one queen. After the cold and rainy summer of 1980, in several nests 3–5 wintering males and winged queens were found.

Most of the ants were usually concentrated in chambers at depths of 20–30 cm under the central part of the dome (Fig. 15). Above this overwintering "nucleus", either isolated ants or small groups of individuals were found. Ants filled the chambers densely, and their number in each chamber was determined only by the size of the chamber. For instance, one of the excavated nests contained

4200 workers with one queen, overwintering in 42 chambers, where the number of individuals varied from 20 to 200. The chambers and tunnels free from ants, as in other species, were filled with large ice crystals.

Formica aquilonia Yarrow, 1955

The range of *F. aquilonia* includes Europe, Siberia and the Russian Far East. In Central Europe this species is rare and occurs only in the mountains; it is common in the northern British Isles and in Scandinavia; in East Siberia it is the most abundant species from the *F. rufa* group (Dlussky, 1967). In West and Central Siberia it prefers dark coniferous, mixed and birch-aspen forests (Omelchenko, 1996; Omelchenko & Zhigulskaya, 1998). In the dark coniferous forests of the northern taiga of the Ob Region its density is at most 2 nests per 100 m² (Omelchenko & Zhigulskaya, 1981). In Yakutia and the Krasnoyarsk Territory it colonizes larch, pine and fir forests, usually in groups (up to 17 nests per ha); isolated nests are typical to the northern boundary of its range (Dmitrienko & Petrenko, 1976). In the Primorye its colonies include up to 50 nests, but their normal average density in spruce-fir forests, from the valleys to their upper altitudinal boundary, is 5–6 per ha (Dlussky et al., 1971; Kupianskaya, 1990).

In the Northeast of Asia this species is recorded on the coast of the Sea of Okhotsk (Zhigulskaya & Berman, 1975; Berman & Zhigulskaya, 1996b), but it has not been found in continental areas of the Magadan Region and in northeastern Yakutia. In the environs of Magadan it colonizes stone birch forests, but only on the terraces of rivers and brooks. In the main part of its range it is a colonial species, but at the coast of the Sea of Okhotsk it is usually found in isolated nests, rarely in groups of 2–3 nests, always confined to open or weakly shaded areas; its nests have not been found on dry south-facing slopes. The highest recorded density of nests is 2 per ha (the upper reaches of the Magadanka River valley), where the size of the nests is normal for flourishing families: around 70–80 cm high and up to 120 cm in diameter.

Formica lugubris Zetterstedt, 1840

F. lugubris is a Palaearctic taiga species, the most cold-loving of the *F. rufa* group. It is mostly confined to spruce forests in European Russia and West Siberia (Dlussky, 1967), found everywhere in the taiga zone of Central and East Siberia (Dmitrienko & Petrenko, 1976), and rarely occurs in clearings in larch forests

in Primorye (Dlussky, 1967); it occupies various forest types of river valleys in Kamchatka (Kupianskaya, 1986b).

In the Magadan Region the ranges of *F. lugubris* and *F. aquilonia* coincide. Both species are absent in continental areas; at the coast of the Sea of Okhotsk they colonize sparse larch forests and stone birch forests, usually in widened kettle-like parts of valleys. Near Magadan, as in Kamchatka (Kupianskaya, 1986b), *F. lugubris* builds small groups of 2–3 nests, confined to open areas of slopes with southern exposure.

ANT POPULATION

The essays on particular species given above show that at the Upper Kolyma ants colonize diverse habitats, avoiding only sedge wetlands, closed forests and high altitude areas (higher than 1300–1400 m above sea level). A high density of ant nests (35–76 per 100 m^2) was recorded in habitats differing widely in hydrothermal, soil and biocoenotic conditions: steppe areas, mixed and broad-leaved forests, sphagnum bogs, sparse forests of various types, Siberian dwarf pine communities, low river spits flooded even by slightly high water etc. (Photo 44). Naturally, high abundance is reached in each of these biotopes by different ant species or their combinations (Table 8).

Three species are especially widespread and occur in different combinations: *Leptothorax acervorum*, *Formica gagatoides* and *Camponotus herculeanus*. These species are among the most visible and most abundant of all the arthropods (except, of course, the blood-sucking flies!) of the Upper Kolyma basin. The density of the former two species reaches 40–44 nests per 100 m^2, and the density of the carpenter ant reaches 4 nests per 100 m^2. In most cases, the nests of *L. acervorum* are prevalent. It is important that all the three mentioned species, absent or very low in abundance in excessively heated and, as a rule, dry localities, flourish in the most typical (zonal) habitats, occupying vast areas of cold and wet biotopes. Even on the northern slopes the total density of these species is 19.5 to 24 nests per 100 m^2 (average values recorded in this biotope are given in Table 8). The abundance of nests was measured according to the method of G. M. Dlussky (1965).

In dwarf-shrub–lichen–moss (usually sphagnum) trains of south-facing slopes with thinned stands of the larch, always slender, in spite of its age (see essay on *Myrmica kamtschatica*), this species complex is almost entirely devoid of *C. herculeanus*, which fails to find in such habitats suitable localities for building its nests. These habitats are co-dominated by *L. acervorum, F. gagatoides* and *M. kamtschatica*. The nests of this *Myrmica* species constitute from 10 to 40% of all
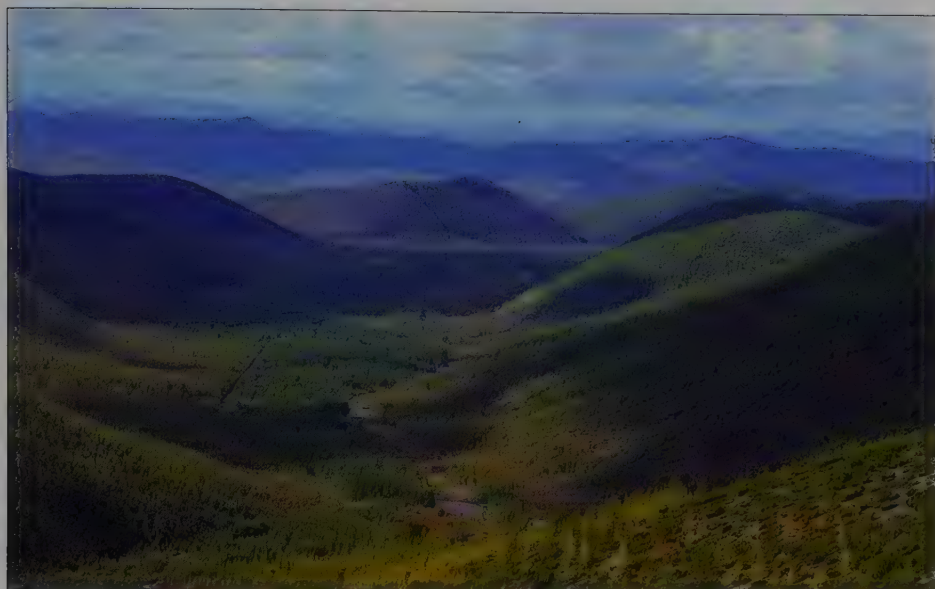
Photo 44. Typical landscape of the upper reaches of the Kolyma, 500–850 m above sea level. The entire visible area is inhabited by ants of the hypoarctic complex (*C. herculeanus, F. gagatoides, L. acervorum*). To the right, clearings of larch forests of south-facing slopes colonized by *F. lemani* and, as everywhere, by the three above-mentioned species. At the bottom of the valley with no talik zone *F. exsecta* and sometimes *F. sanguinea* are common. To the left, in moss communities on the train of north-facing slope *M. kamtschatica* can be found.

the ant nests found on these areas, and it is here that the record density of ant nests in all the examined areas of the Upper Kolyma area, 76 per 100 m², has been observed so far; in some similar small areas nest density is even greater, by a factor of 2–3. In some biotopes of mossy trains, with very large, wet sphagnum "pillows" and high position of the surface of permafrost, both *C. herculeanus* and *F. gagatoides* are absent, and the ant population consists only of *L. acervorum* and *M. kamtschatica*. In such biotopes another species combination, very rare at the Upper Kolyma, was observed: *M. kamtschatica* and *F. candida*.

Dry biotopes of south-facing slopes, such as small steppified areas, grass meadows, meadow post-fire communities (with pasque flower, dragonhead, here and there with dog rose and fireweed), as well as well-drained sparse herb larch forests and aspen forests, rare in the Kolyma area, distinctly stand out in the dominance of *F. lemani*, reaching in these communities the density of 34 nests per 100 m². Essentially, *F. lemani* occupies habitats unsuitable to all the other species because of their excessive dryness. It is accompanied, especially at the edges of these habitats, by *L. acervorum* and *F. gagatoides*. In

Table 8. Ant populations in the principal communities of the sparse larch forest belt

No.	Altitude (above sea level), relief element, inclination	Humidity, vegetation type and projective cover (PC)	Number of nests per 100 m²									
			M. kamtschatica	*F. gagatoides*	*L. acervorum*	*C. herculeanus*	*F. exsecta*	*F. lemani*	*F. candida*	*M. bicolor*	*L. muscorum*	Total
1	2	3	4	5	6	7	8	9	10	11	12	13
		Wetlands, sparse larch forests and Siberian dwarf pine communities, damp and waterlogged										
1	500 m, train of eastern slope, 5–8°	Wetland, dwarf-shrub–sphagnum, with distinct microrelief, PC 100%	16	2	26	+	–	–	–	–	–	44
2	600 m, subhorizontal area	Wetland, sphagnum, without distinct microrelief, PC 100%	6	–	8	–	–	–	–	–	–	14
3	500 m, subhorizontal area	Wetland, moss–cotton-grass–sedge, PC 100%	+	1	7	–	–	–	–	–	–	8
4	500 m, train of southern slope, 5–8°	Sparse forest, damp, dwarf-shrub–sphagnum, canopy density 0.1, PC 100%	23	9	44	+	+	–	–	–	–	76
5	750 m, train of south-eastern slope, 5–8°	Sparse forest, damp, with dwarf pine, moss-lichen, canopy density 0.1, PC 100%	4	14	23	+	+	–	–	–	–	41
6	500 m, train of southern slope, 8–10°	Sparse forest, waterlogged moss-lichen, canopy density 0.1, PC 100%	8	+	17	–	–	–	+	–	–	25
7	550 m, train of southern slope, 8–10°	Sparse forest, waterlogged moss-lichen, canopy density 0.1, PC 100%	5	2	8	–	–	–	–	–	–	15

Table 8. Continued.

1	2	3	4	5	6	7	8	9	10	11	12	13
8	500 m, debris cone of southern slope, 10–15°	Sparse forest, with alder, yernik–grass–cowberry, damp, canopy density 0.1, PC 50%	+	5	8	+	+	–	–	–	–	13
9	500 m, northern slope, 18–20°	Sparse forest, damp, moss-lichen, canopy density 0.1, PC 100%	–	10	10	+	–	–	–	–	–	20
10	800 m, train of eastern slope, 8–10°	Sparse forest, damp, dwarf-shrub–sphagnum, canopy density 0.1, PC 100%	–	4	14	+	–	–	–	–	–	18
11	500 m, subhorizontal area	Sparse forest, waterlogged moss–cotton-grass–sedge, canopy density 0.1, PC 100%	–	+	5	+	–	–	–	–	–	5
12	500 m, subhorizontal area	Sparse forest, waterlogged moss–lichen, canopy density 0.3, PC 100%	–	2	2	+	–	–	–	–	–	4
13	600 m, subhorizontal area	Larch forest, with dwarf pine, lichen–moss–dwarf-shrub, damp, canopy density 0.2, PC 100%	–	40	27	+	+	–	–	–	–	67
14	800 m, subhorizontal area	Dwarf pine community, yernik Labrador-tea–cowberry–moss, damp, PC 80%	–	6	8	+	–	–	–	–	–	14
15	600 m, horizontal area in floodplain	Dwarf pine community, dwarf-shrub–sphagnum–green-moss, damp, canopy density 1.0, PC 45–50%	–	–	–	–	–	–	–	–	–	–
	Sparse larch forests and Siberian dwarf pine communities, mesophyte											
16	650 m, subhorizontal area	Sparse forest, with dwarf pine, lichen–dwarf-shrub, canopy density 0.1, PC 90%	–	20	22	+	+	–	–	–	–	42
17	450 m, subhorizontal area	Cut-over area, larch dwarf-shrub–herb, canopy density 0.1, PC 70%	–	17	20	+	+	–	–	–	–	37

No.	Location	Habitat										
18	800 m, subhorizontal area	Sparse forest, with dwarf pine, dwarf-shrub, canopy density 0.2, PC 60%	–	4	16	+	–	–	–	–	–	20
19	1000 m, southern slope, 25°	Dwarf pine community, lichen–dwarf-shrub, PC 40%	–	2	10	+	–	–	–	–	–	12
20	650 m, subhorizontal area	Dwarf pine community, lichen–dwarf-shrub, drained plateau, PC 100%	–	+	3	+	–	–	–	–	–	3
21	400 m, sandy terrace of the Kolyma	Dwarf pine community, dwarf-shrub–lichen, canopy density 0.4–0.5, PC between bushes 50%	–	11	7	+	2	–	–	–	–	20
22	600 m, subhorizontal area	Dwarf pine community, dwarf-shrub–lichen, canopy density 0.5–1.0, PC between bushes 45%	–	18	7	+	–	–	–	–	–	25
23	810 m, moraine, bank of Jack London Lake	Dwarf pine community, dwarf-shrub–lichen, canopy density 0.5, PC between bushes 70%	–	4	1	+	+	–	–	–	–	5
24	600 m, edge of watershed	Dwarf pine community, dwarf-shrub–lichen, canopy density 0.6, PC between bushes 30%	–	1	2	–	+	–	–	–	–	3
25	700 m, north-eastern slope, 8–10°	Dwarf pine community, moss–lichen–dwarf-shrub, canopy density 0.9, PC between bushes 60%	–	+	+	+	–	–	–	–	–	+
25	700 m, north-eastern slope, 8–10°	Dwarf pine community, moss–lichen–dwarf-shrub, canopy density 0.9, PC between bushes 60%	–	+	+	+	–	–	–	–	–	+
26	700 m, gently sloping watershed	Dwarf pine community, cowberry–lichen–dead-cover, rubbly areas, canopy density 0.2, PC 10%	–	+	+	+	–	–	–	–	–	+

Table 8. Continued.

1	2	3	4	5	6	7	8	9	10	11	12	13
27	850 m, plateau on watershed	Dwarf pine community, complex cowberry–lichen and herb–lichen, closure 0.6, PC between bushes 60%	–	–	3	+	–	–	–	–	–	3
28	1400 m, plateau on watershed	Mountain tundra, dwarf pine, dwarf-shrub–lichen, canopy density 0.1, PC 100%.	–	–	+	+	–	–	–	–	–	+
29	600 m, area in brook floodplain	Dwarf pine community, green–moss– dead-cover, mosaic (in patches up to 100%), canopy density 0.4–0.8	–	–	–	+	–	–	–	–	–	+
30	800 m, north–eastern slope, on watershed, 5–10°	Dwarf pine community, dwarf-shrub– lichen in complex with herb-dwarf- shrub–lichen, canopy density 0.5, PC 50% between bushes	–	–	–	–	–	–	–	–	–	–
	Well-drained communities of south-facing slopes with mesoxerophyte herbaceous cover											
31	500 m, southern slope, 30–35°	Grass–herb steppe, PC 60–80%	–	+	1	–	–	34	–	–	–	35
32	450 m, southern slope, 30–35°	Aspen forest, mesoxerophyte, canopy density 0.3, PC 30%	–	+	1	+	–	21	–	–	–	22
33	450 m, southern slope, 20–25°	Clearings in lichen larch forest, canopy density 0.3, PC 50%	–	–	2	+	–	8	–	–	–	10
34	600 m, southern slope, 30–35°	Post-fire larch forest, grass–herb, PC 80%	–	+	2	+	–	4	–	–	–	6
35	550 m, southern slope, 30–35°	Post-fire larch forest, dwarf-shrub–grass, PC 40%	–	+	2	+	–	1	–	–	–	3

№												
36	650 m, train of southern slope, 7–10°	Dwarf pine community, herb–cowberry, canopy density 0.6, PC of red whortleberry 40–80%	–	38	3	–	+	–	1	–	–	–	42
37	650 m, southern slope, 15°	Dwarf pine community, herb-cowberry, canopy density 0.4, PC 50%	–	10	–	–	–	–	8	–	–	–	18
38	700 m, rubbly south–western slope, 30°	Dwarf pine community, dwarf-shrub–lichen, canopy density 0.5–0.6, PC between bushes 30–40%	–	+	+	–	+	–	+	–	–	–	+
39	700 m, south–western slope, 20°	Dwarf pine community, dwarf-shrub–lichen-grass, canopy density 0.5–0.6, PC between bushes 50–70%	–	+	2	–	+	–	–	–	–	–	2
40	550 m, southern slope, 35°	Grass-herb steppe in Orotuk depression	–	–	–	–	–	–	–	>100*	–	–	>100
41	600 m, southern slope, 15–20°	Grass-herb steppe in Oymyakon depression	–	–	–	–	–	–	–	–	–	>100**	>100
	Pioneer communities of floodplains												
42	480 m, low floodplain	Pebbly areas with young growth of poplar and chosenia	–	–	–	–	–	–	–	>100*	10	–	>100

* Highest number of "nest accumulations" in populations is indicated; ** highest number of nests is indicated;
"+", density lower than 1 nest per 100 m²; PC, projective cover.

the most xerophyte steppe areas of the Kolyma basin (the Orotuk depression and the valley of the Korkodon River) *F. lemani* is absent; these areas are colonized by *F. candida*, which, however, builds its nests not in steppe biotopes, but in adjacent communities, mesophyte erosional depressions. In the still more thermophyte steppes of the Indigirka valley *F. candida* has not been found and the only ant species, often abundant in steppe areas proper, is *L. muscorum* (Berman et al., 1982). Finally, a special community of two species, *F. candida* and *M. bicolor*, as mentioned above, is formed in pebbly and sandy-pebbly areas of the floodplains of large rivers, usually at the edges of poplar-chosenia forests.

An important feature of nest location within virtually any forest biotope is the dramatic decrease of nest density under the canopy of trees or even in the shadow it produces; in closed forests ant nests are extremely rare. This effect doubtlessly reflects the lower temperatures created by shading. The deepest shade is produced by the alder, especially dense stands, but even under isolated alder bushes ants have never been found. They also refrain from occupying dense larch forests, such as post-fire polewoods, even though the larch, a light coniferous species, produces relatively weak shade (Pozdnyakov, 1983). The influence of shade on different ant species is unequal. For instance, in herb–dwarf-shrub sparse larch forests with the Siberian dwarf pine nests of *F. lemani* are usually built in large light clearings, whereas *F. gagatoides*, avoiding the deep shadow of the dwarf pine, copes with the light shadow of young larch trees.

It is no less important that ants, even the most abundant species, build their warming chambers only in larch wood, whereas all the other trees of the Northeast of Asia (Siberian dwarf pine, long-boled birches, alder, poplar, chosenia, *Salix rorida* etc.) are clearly ignored. The causes of this are probably manifold and not entirely clear. In the case of the Siberian dwarf pine, one of the probable unfavourable factors, for instance for *C. herculeanus*, may be the more or less surface position of the skeletal roots of its bushes; with only the lower parts buried in the soil. Overwintering chambers built in larch roots, as well as the overwintering chambers of ground nests under similar conditions, are positioned somewhat deeper, at 5–15 cm. This difference of a few centimetres is probably important for the survival of overwintering ants. It is also possible that the Siberian dwarf pine is more efficiently protected from wood-dwelling insects than the larch by ample production of resins. In any case, even nests of the carpenter ant are relatively rarely found in the dwarf pine. Nests, or rather warming chambers, of *L. acervorum* are found in remains of dwarf pine wood, but also rarely, whereas the warming chambers of this species in larch wood remains are quite common.

All ant species, avoiding the shade of Siberian dwarf pine bushes and refraining from building nests in their wood, not only display no connection with

this plant, but also tend to nest in spaces between its bushes. The Siberian dwarf pine usually colonizes poor and acidic soils, usually covered with equally poor plant communities formed by various mixed types of lichen and dwarf-shrub associations (see Chapter 1). All these factors ultimately result in the depletion of the species composition of ants, and their populations degrade into various combinations mostly of two species, *F. gagatoides* and *L. acervorum*

Thus, the habitat distribution of ants in the study area has the following fundamental generalised pattern. The overwhelming majority of middle altitude areas of the Upper Kolyma are inhabited virtually everywhere by three abundant and prosperous species (*L. acervorum*, *F. gagatoides* and *C. herculeanus*), and for *L. acervorum*, judging by the density of its nests and the diversity of the habitats it successfully occupies, this area is probably the optimum of the range, or, according to K. V. Arnoldi (1957), biotic optimum (see Conclusion). Sparse sphagnum forests and wetlands of the trains of south-facing slopes are co-dominated by *M. kamtschatica*. All the other ant species found in the Upper Kolyma area are mostly confined in their distribution to local habitats with conditions dramatically deviating from those typical of the region in general (i.e. zonal). In such habitats the above-mentioned four species usually give way to others. Mesoxerophyte communities of south-facing slopes are dominated by *F. lemani*, the extremely dry and hot areas of the Upper Kolyma (we should emphasize that they are a unique case) are dominated by *F. candida*, and similar areas of the Indigirka are dominated by *L. muscorum*. *M. bicolor* occurs exclusively in floodplains, together with the abundant *F. candida*. Only one species, *F. exsecta*, undoubtedly mesophile, has wide, but patchy distribution, and its habitat preferences, judging by summer conditions, are not obvious (see Chapter 5).

At the altitudes of 900–1100 m above sea level, i.e. at the zone of transition from sparse forests to mountain tundras, the ant population changes considerably: species richness and abundance decrease, and the scope of occupied habitats narrows. *M. kamtschatica* and *F. lemani* do not reach into this zone; *F. candida* was only once found near the tree line (over 800 m above sea level, in the floodplain of the upper reaches of the Ayan-Yukryakh River, one of the sources of the Kolyma). Northern slopes and plateau-like areas are not colonized by ants at these altitudes; only a few nests of *L. acervorum* were found in such localities. The density of the nests of all species dramatically decreases on west- and east-facing slopes, sometimes to zero. *F. exsecta* reaches into higher altitudes along south-facing slopes, where its isolated nests occur as high as 1200 m above sea level, accompanied by the three species dominant in sparse forests, *L. acervorum*, *F. gagatoides* and *C. herculeanus*. The ant population of these altitudes is heterogeneous or, more precisely, clumped: in favourable localities the density of their nests is as high as in sparse forests at the altitudes 400–600 m,

and in some localities ants are totally absent. Only *L. acervorum* is found at still higher altitudes, up to 1200 m on eastern and western slopes and up to 1400 m on south-facing slopes, where isolated nests of this species are sometimes still found (Berman et al., 1980).

These altitudinal limits are sometimes shifted in areas with peculiar mesoclimate. For instance, they are lower in narrow valleys with strong cover of the soil and higher in the vast depression of Jack London Lake (the surface of which lies at the altitude of 804 m above sea level). Sedge communities (formed by *Carex argunensis*, *C. rupestris* etc.) also pose an exception. They are warm, xeromorphic, sometimes moderately humid, usually occupying watersheds or edges of floodplain terraces, but always in "windproof" localities (Berman, 1990). In spite of the high heat supply, no ants are found in these communities (except in isolated nests at their edges), probably because of their lack of snow and consequent winter-killing.

Thus, at higher altitudes, where heat supply is decreasing, azonal ecosystems and species they include gradually disappear, and zonal ecosystems become prevalent, along with the three ubiquitous ant species (*C. herculeanus*, *L. acervorum* and *F. gagatoides*), in some habitats accompanied by *F. exsecta* (Berman et al., 1980). But this species complex also changes visibly with altitude: the density of nests decreases and the scope of inhabited biotopes narrows. In the first place ants disappear from northern slopes, then from slopes of neutral exposure, reaching into high altitudes only along south-facing slopes.

THE PLACE OF ANTS IN THE SOIL MACROFAUNA COMMUNITY

The picture of the ant population of the study area would be incomplete without discussing the place of ants in the communities of soil macrofauna. Although the examined area is large and the studied ecosystems diverse, only a few fundamental types of such communities and corresponding habitat groups can be recognized on the basis of the structure of dominance (Berman & Bukhkalo, 1985).

I. Absolute dominance of enchytraeids (up to 20 thousand per m²) with considerable proportion of myriapods, sometimes with co-dominant dipteran larvae and relatively low abundance of other arthropods. This type of community is typical of the coldest areas with ice-bearing permafrost (STL around 50–60 cm) covered with a thick layer of soft peat with high porosity, which is an ideal substrate for microscopic arthropods and myriapods feeding on them; surface cover either moss or moss-lichen. The place of ants in communities of this type is quite modest; they are represented here by the three hypoarctic species.

II. Absolute dominance (up to 81% abundance and 75% biomass of all arthropods) of chilopods, sometimes co-dominated by dipteran larvae. Chilopods are represented by two families: Geophilidae and Lithobiidae (the prevalent species is *Dacrobius krivolutzkyi*). Enormous abundance (Tullgren extractions yielded over 400 individuals of both families per m²!) was observed in cold Siberian-dwarf-pine communities with moss cover and in dense alder forests with STL around 60–80 cm. The abundance of ants in this type of communities is still lower than in the preceding type.

III. Absolute dominance of mesophile ants (*Leptothorax acervorum, Camponotus herculeanus, Formica gagatoides* and *Myrmica kamtschatica*): up to 90% abundance and up to 80% biomass, with co-dominant chilopods. Such communities are typical of dwarf-shrub–moss sparse larch forests, usually tussocky or with uneven nanorelief. This community type is essentially the same as the preceding, but colonized by ant species absent there because of shading and underdeveloped nanorelief.

IV. Dominance of xerophile ants (*Formica lemani* and *Myrmica angulinodis*) with co-dominance of beetles, or vice versa, depending on the degree of shading. These communities are typical to xerophyte biotopes and especially developed in steppe areas. In half (by number) of the examined communities beetles are dominant or co-dominant. However, only six of the more than 20 recorded families can be considered dominant: click beetles, ground beetles, soldier beetles, rove beetles, weevils and longhorn beetles.

These four principal types of communities, of course, fail to describe the entire diversity of invertebrate communities observed in the study area, but represent the most common kinds of them. Several especially characteristic communities can be named, confined to peculiar habitats, the total area of which is, however, extremely small. These include the communities of aspen forests and areas of post-fire xeromorphic meadows with absolute dominance of earthworms (*M. angulinodis* occurs in such habitats, as noted above); poplar-chosenia forests with huge proportion of fly larvae, especially Bibionidae (ants are represented by *F. candida* and *M. bicolor*); clumpy alder forests of northern slopes with dominant Tipulidae larvae accompanied by the larvae of small flies etc., with ants totally absent; dwarf-shrub–reedgrass birch forests and floodplain larch forests with superdominant (56–70% arthropod abundance) scale insects, mostly *Arctorthezia cataphracta*, found also in many other communities of the Upper Kolyma.

Communities of the first three fundamental types occupy by far largest part of the area, varying and gradually transforming into each other. The total number of species determining the structure of most such communities of all the soil macrofauna groups is probably at most 25–30 (it should be emphasized that

this refers only to the groups we have studied). Since the vast majority of the area is occupied by various humid and/or cold biotopes with ice-bearing permafrost and relatively thin STL, the oligodominant complex formed mainly of chilopods (2–3 species) and mesophile ants (3–4 species) is generally prevalent in the area. Centipedes of both discussed families are known to be predaceous; ants also require large amounts of protein food for feeding their brood. Thus, the soil macrofauna of huge parts of the area are dominated by obligate and facultative predators feeding on the extremely abundant, especially in mellow peat and peat-like ("dry peat") substrates, microscopic invertebrates.

As for xeromorphic communities, their total area is small, and most of them are dominated by ants.

A most important feature of the soil macrofauna population of the study area is the independence of its structure of the forest tree species prevalent in the region—the larch and the Siberian dwarf pine. In other words, predicting the invertebrate community (including the ant population) based on the dominant tree species is impossible. This reflects the above-noted enormous ecological valence of the larch and the Siberian dwarf pine, which makes them capable of occupying a wide range of localities with soils and permafrost of different types.

The composition of soil macrofauna and dominant ant species in sparse forests, so typical of our study area, is dependent almost exclusively on the relief of particular localities (in areas formed by the same rocks). This predictability undoubtedly reflects the key role of relief in drainage and heat supply, which, in their turn, influence the type of permafrost (ice-bearing or dry), largely determining the type of surface vegetation. The composition and abundance of the invertebrate population (especially of ants), as noted above, are also strongly dependent on the degree of shading produced by any layer of vegetation.

Thus, ants occupy an extremely important place in the soils macrofauna communities of the overwhelmingly largest part of the sparse forest belt in the Upper Kolyma basin.

*   *   *

The above-described pattern of ant distribution refers to continental mountain taiga areas of the Magadan Region, whereas in areas with more continental climate, in northeastern Yakutia, and in areas with less continental climate, closer to the coast of the Sea of Okhotsk, somewhat different patterns are observed. Our reconnaissance of the Oymyakon, the Moma and the Nera depressions in the "standard" continental region, where the boundaries of altitudinal belts, including the tree line, are somewhat shifted, and the Siberian dwarf pine is pushed to higher altitudes than in the Upper Kolyma, showed that the living

conditions of ants in these dwarf-pine communities are suitable only for the three ant species of the zonal complex; no other ant species have been found in these communities so far.

At the coast of the Sea of Okhotsk, where the climate is considerably different from that of the inland areas of the Kolyma basin (Klyukin, 1970), the boundaries of altitudinal belts are shifted in the opposite direction: forests do not reach greater altitudes than 650–700 m above sea level, and dwarf-pine communities are found from sea level to the tops of the mountains, i.e. to 900–1000 m above sea level, on slopes of every exposure, including northern. We have already noted that the ant fauna of the coast is richer. But ants in this area are also confined to sparser forests (larch and stone-birch) and dwarf-pine communities. Most of the ant species, as in the Kolyma area, are found only in the lower parts of slopes. The richness of the ant fauna decreases higher than 200–250 m above sea level on northern slopes and higher than 350–400 m on south-facing slopes, and the ant population of the higher altitudes is constituted, as in the Kolyma, by the ubiquitous *L. acervorum*, *C. herculeanus* and *F. gagatoides*, independently of the vegetation type.

Thus, in spite of considerable differences between the geographical environment of northeastern Yakutia, the upper reaches of the Kolyma and the coast of the Sea of Okhotsk and between the ecological conditions of particular habitats, the formation of ant populations in the dominant communities of these areas (larch and dwarf-pine) is influenced by a small number of common factors. For instance, ants avoid the shade of any "shade-producing" species; their nests and warming chambers are very rarely built in any kind of wood, except in the wood of the larch. Wood of all the other tree species in the Northeast of Asia does not undergo the myrmicid stage of decay. Only rarely the nests of the carpenter ant are found in old dead shoots of the Siberian dwarf pine near the upper altitudinal boundary of its distribution. Species diversity decreases with altitude, and dwarf-pine communities are inhabited only by the dominant hypoarctic complex of ants (Zhigulskaya & Berman, 1989; Berman & Zhigulskaya, 1996a).

CHAPTER 3
OVERWINTERING TEMPERATURE CONDITIONS OF ANTS IN THE UPPER KOLYMA REGION

As shown in the previous chapter, most ant species of the Upper Kolyma overwinter in the surface horizons of the soil, and only a few overwinter deeper than 50 cm. Snow, vegetation, soils and/or ground layers smooth out the temperature conditions, compared to the excessively harsh ones of the air. No more or less reliable descriptions of the temperature regimes under the cover of snow are available, not only for the upper reaches of the Kolyma, but also for the adjacent areas with even colder continental climates. The network of the Hydrometeorological Service carries out measurements of this kind only in a few weather stations, and there is not an adequate body of primary thermophysical data available for a broad application of mathematical methods. Short time-scale observations are insufficient for estimating to what degree the observed picture is typical, since seasonal courses of air temperatures and of the regime of snow accumulation vary considerably from winter to winter. All these reasons convinced us to study in detail the conditions of the upper layers of soils and ground in the most typical biotopes and directly in the ant nests over several winters. To place these results in context, we shall first discuss the factors determining the winter temperature regime of the upper 20 cm layer of the soil and its variations in different biotopes of the altitudinal profile from the valley of the Kolyma to the upper boundary of mountain tundras, and then describe against this background the temperature courses observed in ant nests.

METHODOLOGICAL APPROACHES

The soil temperature in more than 40 typical biotopes and in large ant nests was measured with specially damp-proofed standard resistance sensor thermometers (TSM) with nominal resistance 53 and 100 Ω together with a P-333 conducting bridge, as well as special meteorological sensors with resistance 270 Ω and

AM-29M loggers. The temperature in small nests was measured with small hand-made thermometers of smaller resistance placed in the nests. Sensors were usually installed in summer, and temperature registration continued for 2–3 years. In winter measurements were taken once in every 5–7 days. Results of twenty-four-hour measurements of air and soil temperatures with KSM-4 12-pixel logger bridges, which allowed determiniation of the position of single temperature measurements on the curves of daily and seasonal temperature courses, were used for greater reliability of the interpretation of data sequences obtained this way. Logger bridges were installed in four typical biotopes: sphagnum–dwarf-shrub larch forest on the train of an east-facing slope with a nest of *Myrmica kamtschatica*; sphagnum–dwarf-shrub larch forest on the drift of a south-facing slope, near a nest of *Formica candida*; meadow area of a dry south-facing slope with nests of *F. lemani*; and sphagnum–dwarf-shrub larch forest on a north-facing slope. In addition, in almost all of the sites where seasonal courses of temperature were measured and in a number of typical biotopes the lowest seasonal temperatures were measured with minimum thermometers at depths of 0–1, 5, 10, 20, 40 and 60 (and deeper, in cases of thicker seasonal thawing layer) over two or more years. The precision of all temperature measurements was 0.5 °C.

The thickness of the snow cover was measured with measuring rods precisely at the sites where thermometers were installed; snow-measuring (Nastavlenie…, 1969) was carried out for describing the snow cover more thoroughly. In addition to these investigations, data measured for many years at nearby meteorological stations (Spravochnik…, 1966) and our data on the air temperatures along the altitudinal profile from the bottom of the Kolyma valley to mountain tundras were used for the description of the temperature field of the soils and earth. Most measurements were taken from 1976 to 1982. In winter almost identical temperatures are observed in nests with cones of piled-up plant debris, for instance of *F. exsecta*, and at the same depth near them, and the temperatures in ground nests and at the same depth in the soil near them are also equal. For this reason, in most biotopes we estimated the temperature regime in the overwintering chambers of ants from the temperature courses observed in corresponding levels of soils and ground. At the same time, the conditions within any biotope are heterogeneous because of the patchy character of vegetation, characteristics of the snow cover, etc. For this reason, seasonal temperature courses were also measured directly in the nests of most ant species, to ensure greater reliability of our data. For instance, these courses were measured in four nests of *F. exsecta*, three of which were in a sparse larch forest with willow undergrowth on a terrace of the Olen Brook (500 m above sea level) and one in mountain tundra on a south-facing slope (1300 m above sea level); in

nests of *Leptothorax acervorum* at the same sites as in *F. exsecta* and in a sphagnum–dwarf-shrub larch forest at an altitude 500 m (a total of eight nests); in nests of *F. gagatoides* at all the above-listed sites and additionally on a dry rubbly south-facing slope with meadow vegetation (a total of five nests); in four nests of *M. kamtschatica* in a sphagnum–dwarf-shrub larch forest on the train of an east-facing slope (500 m above sea level); in three nests of *F. candida* in a sphagnum–dwarf-shrub larch forest on the train of a south-facing slope. Nests of *Camponotus herculeanus* were studied in a stump and in three fallen larch trees, all in different localities of a terrace of the Olen Brook. The conditions in nests of *L. muscorum* were estimated by measurements of the soil temperatures on a steppe slope in the valley of the Uchugey River 3 km from where it flows into the Agayakan River (left-hand tributary of the Indigirka) near the meteorological station of the same name (August 1977 – September 1978). The winter conditions in nests of *M. bicolor* and *F. candida*, which colonize only floodplain terraces, often in immediate proximity to each other, were studied in the floodplain of the Detrin River at the edge of a poplar-chosenia forest, around a nest of *M. bicolor*. In addition, the temperatures in four nests of *F. exsecta*, two nests of *F. gagatoides* and one nest of *L. acervorum* in sphagnum–dwarf-shrub larch forests in the depression of Jack London Lake at an altitude of 850 m above sea level were measured for three days in late February 1980. Later it was found that these measurements were taken during the last very cold period of the winter, with temperatures below –40 °C, so it is safe to consider the recorded conditions close to the extreme.

We used the lowest seasonal values of temperatures in soil horizons 0–1, 5, 10, 20 and 40 cm deep as the main parameter of the winter temperature regime in the studied biotopes, because these temperatures are potential limiting factors for the existence of ants. However, since almost all of the extreme values were obtained either by minimum thermometers or by single measurements with electrothermometers, we could not estimate the typical duration (hours or days) of the lowest temperatures and, thus, could not use these measurements in describing the winter ecology of ants. But processing the record charts of loggers showed that in the areas of especially low temperatures the daily ranges of temperature at the depth of 10–20 cm even under thin cover of snow were usually no greater than 0.3–0.5 °C. In other words, considering the precision of our measurements (0.5 °C, as indicated above), we might safely assume that the duration of lowest temperatures was around 24 hours. It is this time scale that determines the survival rate of most groups of invertebrates, since mortality from long (16 hours to 20–30 days) exposure to low temperatures is not strongly dependent on the duration of exposure (Salt, 1966b; Merivee, 1972; Kuusik, 1970).

The temperature conditions of the soil during the cold season depend on air temperature, thickness and density of the snow cover, type of vegetation, water content (or iciness) of the soil and the heat supply of its deeper horizons. The first three of listed factors have an especially strong impact on the lowest temperatures of surface horizons, whereas the type of vegetation and the humidity of the ground largely determine the pattern of freezing. The heat supply of the deeper horizons usually has no impact on the temperature regime of the upper layers (Alfimov, 1984, 1985, 1989); this phenomenon is discussed in more detail in the section describing the winter conditions of talik zones.

AIR TEMPERATURE

The winter climate of the Upper Kolyma basin is determined, on the one hand, by the proximity of the northeastern branch of the Siberian High with its coldest winter temperatures of the Northern Hemisphere, and, on the other hand, of the cyclones coming into this area and bringing about warming, winds and snowfalls. The alternation of such contrasting regimes leads to considerable deviations, sometimes as great as 8–10 °C, of average monthly temperatures from their long-term average values. The magnitude of these deviations allows the upper reaches of the Kolyma (together with the Yukon basin) to be considered a region with the most variable weather in the Northern Hemisphere, both in a single winter and at the long-term scale (Gedeonov, 1967). Average long-term air temperature at the Aborigen Field Station (500 m above sea level), determined by comparison with the data of nearby meteorological stations from a 10-year sequence of measurements (Chelpanova, 1963), is −32.6 °C in December, −34.1 °C in January and −31.0 °C in February. The variation of the average annual values of the lowest air temperatures measured at nearby meteorological stations (Spravochnik…, 1966) is similar (2-3°). The averaged results of measurements taken during the same months over the period from 1978 to 1981 are −37.7, −29.9 and −28.4 °C, respectively. Thus, during the years when our studies were carried out, Decembers were considerably colder, Januaries considerably warmer and Februaries close to the average (Alfimov, 1985). As a result, the lowest seasonal air temperature may be observed at virtually any time from the end of November to the end of February, and this phenomenon has a profound impact on the seasonal courses of soil temperatures.

During the anticyclonic weather regime the downflow and stagnation of cold air masses into intermountain depressions strengthen the vertically inverted distribution of air temperatures caused by the radiation cooling of the surface. The greatest vertical gradients are observed in lower parts of

the mountains (at altitudes of 500–800 m above sea level): average 10-day temperatures in this area sometimes increase as much as 3.6 °C per 100 m of altitude. The resulting difference between the tree line and the bottoms of valleys is 12 °C (Alfimov, 1984). At higher altitudes the gradient weakens and disappears at 1250–1300 m above sea level. During cyclonic weather, which brings about warming and stronger winds, this inverted pattern of temperature distribution is disrupted.

The most important impact of the inverted temperature pattern on wintering organisms is the "cutting" of particularly low temperatures at higher altitudes. In mountain tundras at 1250 m we never recorded temperatures lower than –37 °C, while at 500 m the lowest temperature recorded was –54 °C, and at 350 m it was –59 °C. These values are close to the climatic parameters of the region in general: the average annual minimum values recorded at nearby meteorological stations standing in the same altitudinal belt vary from –40 to –56 °C (Spravochnik…, 1966).

The impact of slope exposure is negligible against the background of these altitudinal temperature changes: the variance of 10-day averaged temperatures is no greater than ±1.2 to 1.5 °C, and lower parts of northern and southern sides of the valley where our measurements were taken were sometimes warmer and sometimes colder than the bottom of this valley (Alfimov, 1984).

SNOW COVER

At lowest air temperatures close to –60 °C the factors preventing the soil from cooling, especially the course of accumulation and pattern of spatial distribution of the snow cover, are particularly important for the formation of soil conditions. Relatively low (100–200 mm) amounts of solid precipitation are typical of the continental areas of the Northeast of Asia, which results in the average thickness of snow being 30–40 cm during the coldest months, increasing by March to 40–50 cm (Klyukin, 1970). However, the values of these parameters may vary considerably from year to year. For instance, the greatest thickness of snow cover recorded in winter at the Ust-Omchug Meteorological Station, 90 km from the site of our work, is usually around 28 cm, but in some years it varies from 16 to 53 cm (Spravochnik…, 1968). The amount of solid precipitation depends a lot on altitude: it increases by 2–3% with every 100 m on windward macroslopes and by 5–7% on leeward macroslopes (Klyukin, 1970), and this factor also influences the thickness of the snow cover.

The unevenness of the snow cover in biotopes is created at one and the same altitude mostly by winds by means of snowdrift, with vegetation, especially

shrubs and dwarf-shrubs, not only increasing the thickness of snow, but also decreasing its density.

The smallest snow thickness (0–20 cm) and the most uneven distribution of snow in the sparse forest belt is observed in areas of trains, terraces and upper parts of slopes with different exposure open to the action of winds and lacking shrubs and trees. In mountain tundras, where wind speeds are considerably greater, such areas are almost invariably snowless. The greatest snow thickness with most even distribution is recorded in localities protected from winds: on slopes and terraces covered with forest, in brook valleys and lake depressions, and on leeward south-facing slopes above the tree line. In other biotopes medium values of snow thickness, 20–40 cm, are observed. The variance of snow thickness within a single biotope, an important feature of the snow cover, is in most cases 60–80 cm. Considerable increases in snow thickness within an area can be caused by the accumulation of snow in windless localities at bends of slope surface, clumps of trees etc., as well as in various meso- and microrelief features: erosional depressions, areas of thermokarst subsidence of permafrost, beds of temporary watercourses etc. The smallest thickness of snow within a biotope is observed in positive areas of the microrelief: tussocks, frost blisters (blow-ups) etc. However, the unevenness of snow cover distribution is only rarely reflected in the unevenness of vegetation. The above-mentioned sedge communities, usually marking snowless areas, and *Rododendron aureum*, which, on the contrary, survives only completely covered with snow, can be considered among the few examples. The dependence of the Siberian dwarf pine on snow is also quite strong: branches protruding from the snow get "frost-burned": their needles turn yellow and die off in spring.

The thickness of snow in most biotopes of the sparse forest belt increases rather smoothly from the moment of snow cover formation to the start of snow melting. Considerable variance can be observed only in areas open to the action of winds. In the mountain tundra belt, on the contrary, the greatest thickness of snow is observed within 10–20 days after the formation of snow cover, and afterwards it only rarely varies due to compression and wind redeposition (Alfimov, 1984).

It is well known that the heat-insulating effect of snow depends not only on the thickness of the snow cover, but also on its density. In sparse forests the lowest snow density (up to 0.13 g/cm^3) is found in areas protected from the wind, and the highest snow density was recorded in forest-free wetlands and on terraces. Thus, since snow density is usually high where its thickness is small, the insulating effect of snow in different localities can vary to a greater degree than either snow density or snow thickness.

In the mountain tundra snow thickness is, on the average, greater than in sparse forests, and the pattern of its density distribution differs from that

found in sparse forests in still greater unevenness, including unevenness within a single biotope. In snowdrifts, alterations of layers with different density, from extremely dense snow (density over 0.40 g/cm³) to loose recondensed powdery layers, are observed. Such heterogeneity increases the heat-insulating capacity of the snow (Pavlov, 1979), somewhat compensating the effect of higher average density and helping to decrease the cooling of areas covered with snowdrifts.

LOWEST SOIL TEMPERATURES

The combined action of air temperature, snow thickness and density, surface cover, soil water content and a number of other factors determines the forma-tion of a pattern of soil temperatures continuous at any given moment of the cold season, not excepting the periods of extreme temperatures (Fig. 16). The grouping of areas according to the lowest values (Fig. 17) shows that the depth of snow greater than 40 cm is a sufficient condition for keeping soil tempera-tures at the depth of 0–1 cm no lower than –25 to –26 °C (and a the depth of 20 cm no lower than –19 to –20 °C). The absence of snow, on the contrary, leads to the cooling the soil to –40 to –48 °C in the upper cm of and to –39 to –40 °C in the 20 cm horizon. These extreme cases are found in less than half of all the studied biotopes, whereas most biotopes (and the overwhelmingly largest part of their area) have medium snow thickness and, thus, lowest soil temperatures –22 to –32 °C at the surface and –16 to –24 °C at a depth of 20 cm.

The variation of the values of these parameters within the recognized groups and their overlapping between groups result from the impact of factors other than snow thickness (such as air temperature, type of surface cover, soil water content etc.) on the formation of the soil temperature field. It is especially dif-ficult to separate the influence of soil water content and vegetation type. How-ever, for thermophysical reasons, the water contained in the soil not only helps to slow down the dropping of temperatures below 0 °C by releasing the latent heat of crystallization in the course of freezing, but also, after turning into ice, increases the heat capacity and the heat conductivity of the soil, improving the transmission of heat from permafrost layers with constant temperatures around –5 to –7 °C and thus impeding cooling and increasing the extreme values. In addition, increases in the projecting cover of vegetation not only contribute to the accumulation of greater amounts of snow, but usually also indicate the pres-ence of relatively thick organogenic horizons, which have low heat conductivity, which also has impact on the temperature regime of the soil.

The combined effect of such hard to separate factors as soil water content, vegetation type and snow cover thickness has an especially great impact during
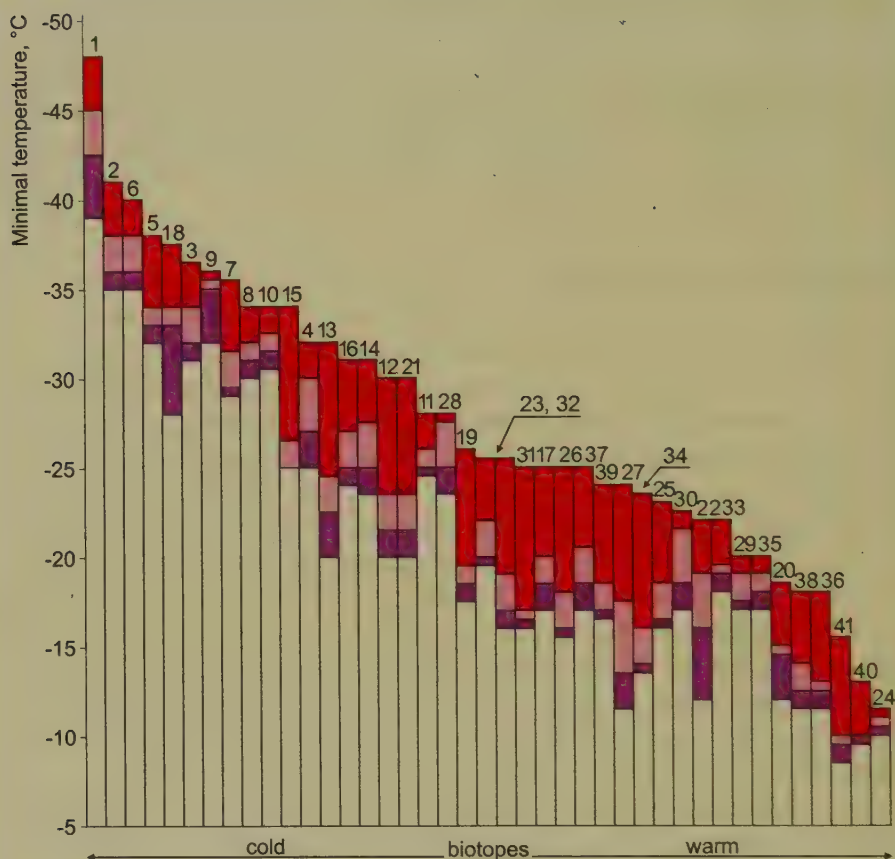
Fig. 16. Lowest soil temperatures of the examined areas. Red columns, temperature change in the upper 5 cm of soil; pink, at a depth of 5–10 cm; lilac, 10–20 cm. The figure above the column indicates the number of the area in Table 8.

the first half of winter, prolonging the period of the freezing of the upper soil layer in wet biotopes with thick snow cover in the sparse forest belt to 20 days, and in mild and snowy winters to 1.5–2 months. After freezing, the soil in such areas gradually cools for 4–4.5 months, and the lowest temperatures are usually recorded in the second half of winter, sometimes even in late February or early March.

The courses of air and soil temperatures in dry areas, especially with thin snow cover, are strongly correlated. The crossing of 0 °C sometimes takes about a week, and the lowest soil and air temperatures are recorded simultaneously. Thus, the greatest difference between dry and wet soils is observed during the first half of winter and, other factors being equal, reaches 6–7 °C. The cooling of

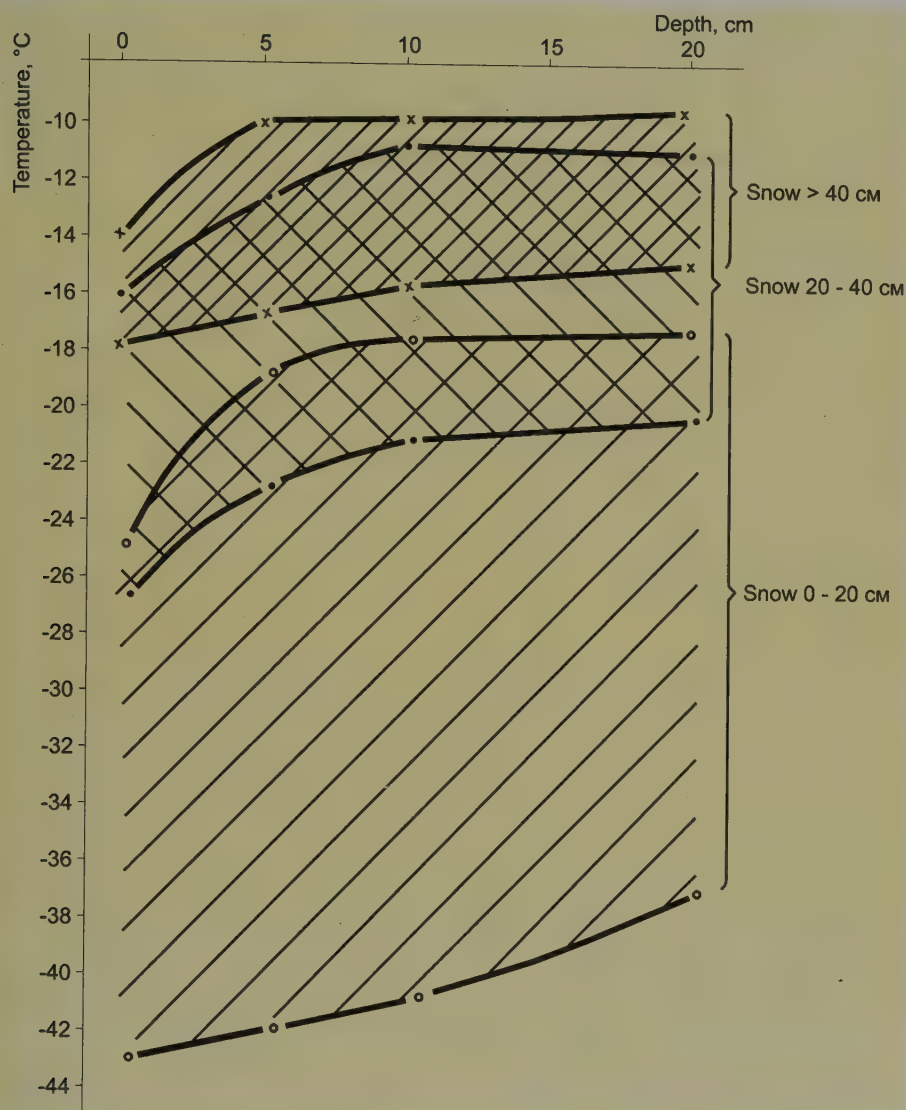**Fig. 17.** The range of lowest soil temperatures in biotopes with different depth of snow cover.

the soil during the second half of winter is close to extreme in wet areas, while in dry areas the soils warm somewhat, following the air, and this difference decreases to 2–4 °C.

The impact of vegetation in the mountain tundra belt is restricted to retaining small amounts of snow in plateau-like areas. The impact of soil water con-

tent on the formation of the temperature regime of the surface horizons in the mountain tundra belt is also considerably weaker than in the sparse forest belt, because the values of this parameter in late autumn fluctuate within a narrower range and never exceed 70%. The heat released during water crystallization prolongs the process of soil freezing to 1–2 weeks. This is not much compared to the 7–8 weeks under snowdrifts, the position of which is determined exclusively by the relief. As a result, the range of soil temperatures in each group of biotopes, recognized on the basis of snow thickness, is narrower than in biotopes of the sparse forest belt, reflecting the higher air temperatures and the lower diversity of humidification and vegetation conditions in the mountain tundras.

The combined action of all the factors creates the following pattern of the distribution of the lowest soil temperatures in typical landscapes of the upper reaches of the Kolyma (Table 9). Naturally, the "warmest" of all the studied areas are a few with thick snow cover and high humidity, where the temperatures along the entire profile, except the surface, never decrease lower than −10 to −13 °C (36, 40[1]). However, it is known that the heat conductivity of snow cover depends logarithmically on its thickness (Pavlov, 1979), and the temperatures are not much higher under a metre-thick layer of snow than under a 50–60 cm layer. Thus, in the sparse forest belt those areas where the thickness of the snow cover is not the highest recorded, but the soil is fairly humid (39, 37, 35, 30, 26) can still be considered "warm". Therefore we may consider the snow thickness of 40–50 cm the lower limit defining "warm" biotopes. The soil temperatures of such habitats never drop lower than −18.5 °C a depth of 10 cm. By contrast, in areas with soil water content lower than the average, even with snow cover thickness over 40 cm, the soil sometimes cools to −24 to −26 °C at the upper cm, and to −16 to −17 °C at 20 cm (17, 25, 32). In mountain tundra the lowest temperatures under snowdrifts fall within a relatively narrow range: from −18 to −22 °C in the upper cm to −11 to −18 °C at 20 cm (20, 29, 33, 38). The lowest temperatures in the upper 20 cm layer of soil under the bigest snowdrifts, which melt only in midsummer, never drop lower than −11 to −12 °C (24).

The second group of biotopes (with 20–40 cm snow cover) is also divided into subgroups according to soil water content (see Fig. 17). In the mountain tundra belt areas with medium snow cover thickness are rare and represented by only two areas (11, 16), slightly different in humidity and lowest temperatures (−28 to −31 °C in the upper cm and −24 to −25 °C at 20 cm). In sparse forests the biotopes with medium soil water content fall within the range from −23 to −24 °C in the upper cm to −13 to −16 °C at 20 cm (31, 34), which does not overlap with the values recorded in areas with thick snow cover. Generally, the

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[1] Numbers in brackets indicate the numbers of areas in Table 9.

Table 9. Lowest temperatures in the upper layers of the soil in different biotopes

No.	Altitude (above sea level), exposure, position on slope, inclination	Degree of humidity, vegetation type	Maximum snow cover thickness, cm	Lowest temperature (°C) at depth (cm)			
				0–1	5	10	20
1	2	3	4	5	6	7	8
1	650 m, subhorizontal area	Dry rubbly area, sedge (*Carex argunensis*), crustose lichens, PC 5–10%	1–3	–48.0	–45.0	–42.5	–39.0
2	850 m, upper part of northern slope, 30–35°	Dry rubbly scree, crustose lichens, PC 5–10%	0–1	–41.0	–38.0	–36.0	–35.0
3	1300 m, subhorizontal area	Frost polygon (melkozem part). Vegetation and snow absent, surface dry	0–1	–36.5	–34.0	–32.0	–31.0
4	500 m, middle part of southeastern slope, 40°	Dry area of grass-herb-steppe, PC 50–70%	1–10	–32.0	–30.0	–27.0	–25.0
5	1300 m, subhorizontal area	Dry area, melkozem scant, lichens, PC 60%	0–1	–38.0	–34.0	–33.0	–32.0
6	850 m, upper part of southern slope, 20–22°	Dry rubbly scree, melkozem scant, crustose lichens, PC 5–10%	0–1	–40.0	–38.0	–36.0	–35.0
7	1350 m, upper part of southern slope, 24°	Dry dryas–sedge area, PC 60%	0–30	–35.5	–31.5	–29.5	–29.0
8	1650 m, subhorizontal area	Dry flat part of ridge, melkozem scant, various lichens, PC 90%	10–15	–34.0	–32.0	–31.0	–30.0
9	850 m, upper part of northern slope, 30–35°	Moss–lichen communities with dry sphagnum tussocks 20–30 cm high, PC 100%	3–5	–36.0	–35.5	–35.0	–32.0
10	1250 m, subhorizontal area	Wetland, with moss–sedge–cotton–grass communities on tussocks and mosses in hollows, PC 100%	7–10	–34.0	–32.5	–31.5	–30.5

Table 9. Contibued.

1	2	3	4	5	6	7	8
11	1600 m, upper part of northern slope, 18–20°	Damp area, average amount of melkozem, mosses, lichens, sparse dwarf-shrubs, PC 100%	30–50	–28.0	–26.0	–25.0	–24.5
12	500 m, middle part of southern slope, 30°	Dry sparse larch forest, canopy density 0.2–0.3, herbaceous cover, PC 40%	30–40	–30.0	–23.5	–21.5	–20.0
13	350 m, floodplain terrace of the Kolyma	Bog, cotton-grass–sphagnum, PC 100%	30–35	–32.0	–24.5	–22.5	–20.0
14	550 m, middle part of southern slope, 30–35°	Dry melkozem area, with young growth of dwarf-shrubs and herbaceous plants, post-fire, PC 40%	30–50	–31.0	–27.5	–25.0	–23.5
15	475 m, fluvial terrace of a brook	Moss–sedge–cotton-grass wetland in brook valley, PC 100%	10–15	–34.0	–26.5	–25.0	–25.0
16	1400 m, lower part of eastern slope, 15–18°	Dry area, melkozem abundant, lichens, sparse shrubs and dwarf-shrubs, PC 100%	30–35	–31.0	–27.0	–25.0	–24.0
17	400 m, floodplain terrace of the Kolyma	Siberian dwarf pine tangles on dry sandy terrace, lichen–dwarf-shrub cover, PC 60%	50–60	–25.0	–20.0	–18.5	–17.0
18	850 m, upper part of northern slope, 30–35°	Damp moss–lichen sparse larch forest with canopy density less than 0,1 and PC 100%	5–10	–37.5	–34.0	–33.0	–28.0
19	450 m, middle part of southern slope, 30–35°	Dry grassland of *Calamagrostis purpurescens*, PC 50%	30–35	–26.0	–19.5	–18.5	–17.5
20	1250 m, middle part of southern slope, 20–25°	Dry area, melkozem scant, lichens, *Phyllodoce*, *Loiseleuria*, *Spiraea*, PC 55%	60–70	–18.5	–15.0	–14.5	–12.0
21	450 m, middle part of southern slope, 20–25°	Dry larch forest with canopy closure around 0.3, surface cover of lichens, PC 50%	30–35	–30.0	–23.5	–21.5	–20.0
22	500 m, foot of southern slope, 8–10°	Sphagnum tussock in damp moss–dwarf-shrub thinned stand of larch. Canopy density less than 0.1, PC 100%	30–40	–22.0	–19.0	–16.0	–12.0

23	500 m, foot of northern slope, 18–20°	Damp moss-lichen sparse larch forest with canopy closure around 0.1, PC 100%	50–60	−25.5	−22.0	−20.0	−19.5
24	1650 m, upper part of southern slope, 15–18°	Damp area, average amount of melkozem, lichens, sparse dwarf-shrubs, PC 100%	>180	−11.5	−11.0	−10.5	−10.0
25	450 m, floodplain terrace of the Kolyma	Pebbly and sandy floodplain with poplar-chosenia herb community, canopy density around 0.8, PC 60%	45–55	−25.0	−20.5	−18.5	−17.0
26	550 m, middle part of southern slope, 25–30°	Damp herb birch forest, canopy density around 0.3, PC 100%	40–50	−23.0	−18.5	−16.5	−16.0
27	380 m, floodplain terrace of the Kolyma	Dry sandy levee, young growth of larch, canopy density 0.3, lichen-herb cover, PC 70%	45–50	−24.0	−17.5	−13.5	−11.5
28	500 m, middle part of southern slope, 30–35°	Dry grass-herb steppe, PC 70%	25–50	−28.0	−27.5	−25.0	−23.5
29	1300 m, upper part of southern slope, 15–20°	Damp area, melkozem abundant, lichens, sparse shrubs and dwarf-shrubs, PC 100%	90–110	−20.0	−19.0	−17.5	−17.0
30	650 m, subhorizontal area	Dry plateau with tangles of Siberian dwarf pine with lichen-dwarf-shrub cover, PC 100%	45–70	−22.5	−21.5	−18.5	−17.0
31	750 m, middle part of eastern slope, 20–22°	Dry area, Siberian dwarf pine tangles, with canopy density 0.3–0.4, moss-lichen, PC 70%	35–50	−25.0	−17.0	−16.5	−16.0
32	450 m, middle part of southern slope, 30–35°	Dry area, aspen forest, dead cover, with canopy density 0.3, PC 70%	45–75	−25.5	−19.0	−17.0	−16.0
33	1275 m, middle part of southern slope, 20–25°	Dry area, melkozem scant, lichens, *Cassiope, Loiseleuria, Spiraea*, PC 100%	50–60	−22.0	−19.5	−19.0	−18.0
34	380 m, floodplain terrace of the Kolyma	Dry area. Sparse larch forest on pebbles, canopy density 0.1, birch, lichen, dwarf-shrubs, PC 90%	35–40	−23.5	−16.0	−14.0	−13.5
35	500 m, foot of southern slope, 8–10°	Waterlogged moss-lichen-dwarf-shrub sparse larch forest with canopy density 0.1, PC 100%	40–50	−20.0	−19.0	−18.0	−17.0

Table 9. Contibued.

1	2	3	4	5	6	7	8
36	500 m, middle part of southwestern slope, 20°	Damp larch forest with admixture of alder and birch, canopy density 0.3, mosses, dwarf-shrubs, PC 90%	55–60	–18.0	–13.0	–12.5	–11.5
37	750 m, middle part of eastern slope, 15–20°	Damp sparse larch forest, moss–lichen, canopy density less than 0.1, Siberian dwarf pine, PC 100%	40–55	–25.0	–18.0	–16.0	–15.5
38	1300 m, middle part of southern slope, 28°	Dry area, melkozem scant, *Cassiope, Loiseleuria, Phyllodoce*, PC 60%	100–170	–18.0	–14.0	–12.5	–11.5
39	400 m, foot of southern slope, 5°	Damp alder forest, canopy density 0.8, surface cover of cowberry, PC 100%	40–50	–24.0	–18.5	–17.0	–16.5
40	500 m, foot of southern slope, 8–10°	Waterlogged moss–lichen–dwarf-shrub sparse larch forest, closure less than 0.1, PC 100%	50–55	–13.0	–10.0	–10.0	–9.5
41	480 m, terrace of brook	Moderately damp larch forest with young growth of willow in riverbank part of terrace, herbs, dwarf-shrubs, PC 60%	45–50	–15.5	–10.0	–9.5	–8.5

range of temperatures observed in biotopes with medium thickness of the snow cover is extremely wide: from −22 to −32 °C at the surface and from −12 to −23 °C at the depth of 20 cm (12, 13, 14, 19, 22), which overlaps with the values recorded in many of the above-mentioned areas. The degree of surface cooling is equal in many biotopes with medium snow cover thickness, even in localities as different as a moss tussock and a dry rubbly slope.

The third group includes, as mentioned above, snowless areas in sparse forests and mountain tundras. In the coldest of them, found in the sparse forest belt, the lowest temperatures drop as low as −36 to −48 in the upper cm of soil and −32 to −39 °C at 20 cm (1, 2, 6, 9, 18). Similar areas in mountain tundras are somewhat warmer, due to the higher air temperatures: from −35 to −38 to −29...−32 °C, respectively (3, 5, 7).

We shall discuss in somewhat more detail the winter conditions of talik areas, the only habitats where *F. candida* and *M. bocolor* build their nests. Talik is the accepted name for an area situated in the permafrost zone with above-zero average annual temperatures of the soil and the ground. In climates with average annual air temperature lower than −4 to −5 °C, above-zero average annual soil temperatures reflect relatively mild winter conditions, created by non-freezing surface watercourses and by outflows of subpermafrost waters. The degree of the warming effect of water depends on snow cover thickness, strength of the watercourse, granulometric composition of the deposits filtering the water flow, and other factors. Measurements of temperatures under the annual ice cover − the aufeis − in the floodplain of the Olen Brook, where the underflow never stops even at the lowest air temperatures, showed that in winter the distribution of temperatures in the bed of the aufeis shows considerable variation even within distances of several dozen metres (Fig. 18, Photos 45, 46). Judging by the thickness of ice, profiles I and II were close to localities with concentrated underflow, which partly contributed to the formation of the aufeis, whereas profile III (with ice thickness no greater than 20 cm) was near the edge of the aufeis field. In the second half of December, when a 1 m layer of the ground became completely frozen, normal winter stratification (with temperatures increasing with depth) was established only in profile I. The lowest temperatures in profile II at a depth of 60 cm were 1.4 °C higher than at 80 cm and equal to the lowest temperatures at 100 cm. The entire studied layer at the edge of the aufeis was strongly cooled, although vertical temperature gradients were virtually absent deeper than 40 cm (extreme values differed by no more than 1 °C). Comparison of these results with the pattern of lowest temperatures of all the studied biotopes (Figs. 16 and 18) shows that areas in the central part of the aufeis belong to the medium part of the distribution, whereas the edges of the aufeis are close to the cold margin. Thus, the only

Photos 45, 46. Remains of aufeis in the upper reaches of the rivers Anmangynda (above) and Dandychan in July 2006. In spring such aufeis fields, forming in freezing riverbeds from waters rising to the surface, sometimes occupy the whole width of river and brook valleys. They are very common in the Northeast of Asia. Aufeis fields serve as giant traps for flying insects alighting on the ice; they are sometimes covered with ants during reproductive flights.
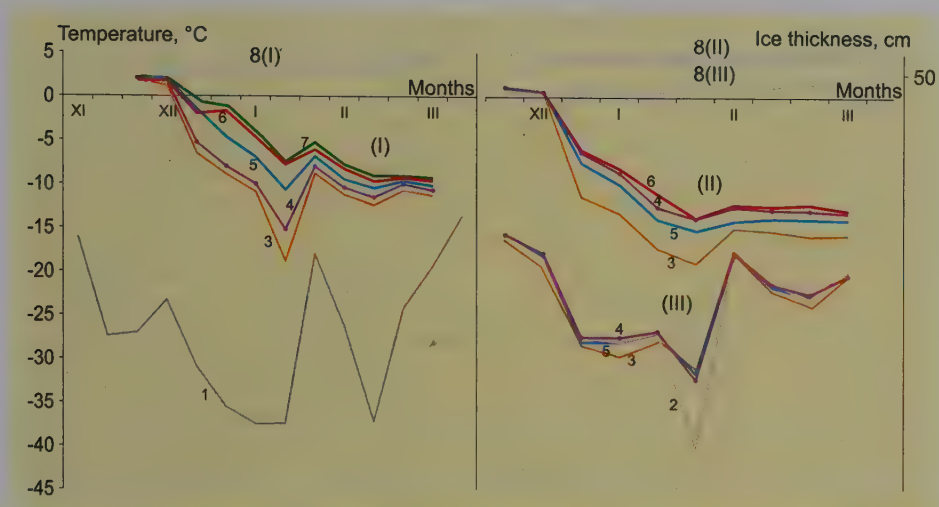
Fig. 18. Seasonal changes of air and ground temperatures along the profiles I–III under the bed of an aufeis of the Olen Brook in the winter of 1989–1990. Average 10-day air temperature, 1; ground temperature, measured every 10 days at the depth of 20 cm, 2; 40 cm, 3; 60 cm, 4; 80 cm, 5; 100 cm, 6; 120 cm, 7; ice thickness, 8.

effect of the underflow on the temperature of the aufeis bed is the increase in the lowest temperatures of the ground at a depth of 60 cm by 3–4 °C, which is unlikely to have any impact on the biota.

Such are the wintering conditions of insects in biotopes of the floodplains of large rivers with uninterrupted water flow. Considerable decreases of water level during winter low waters stop the heating effect of the flow on the surface horizons of the soil. For instance, in the soil of a poplar-chosenia forest, doubtlessly indicating the presence of a water-bearing talik (Nekrasov, 1967), with snow cover thickness 45–50 cm in the floodplain of a secondary tributary of the Kolyma (the Vakkhanka River) the lowest temperature at a depth of 20 cm equalled that in permafrost biotopes with the same snow cover thickness. By contrast, on low terraces of non-freezing to bottom brooks, or in localities with outflowing groundwaters, the impact of the talik is sometimes distinct even in the upper 20 cm of the soil. Fig. 19 shows that talik areas have significantly higher values of the lowest soil temperatures, compared to permafrost biotopes (Alfimov, 1989). The impact of the talik was strongest not in river or brook floodplains, but in an area of a train with shrub alder near outflows of deep groundwaters at sites with anthropogenic disturbances. This impact resulted in a considerable (by 10 °C, compared to permafrost biotopes with
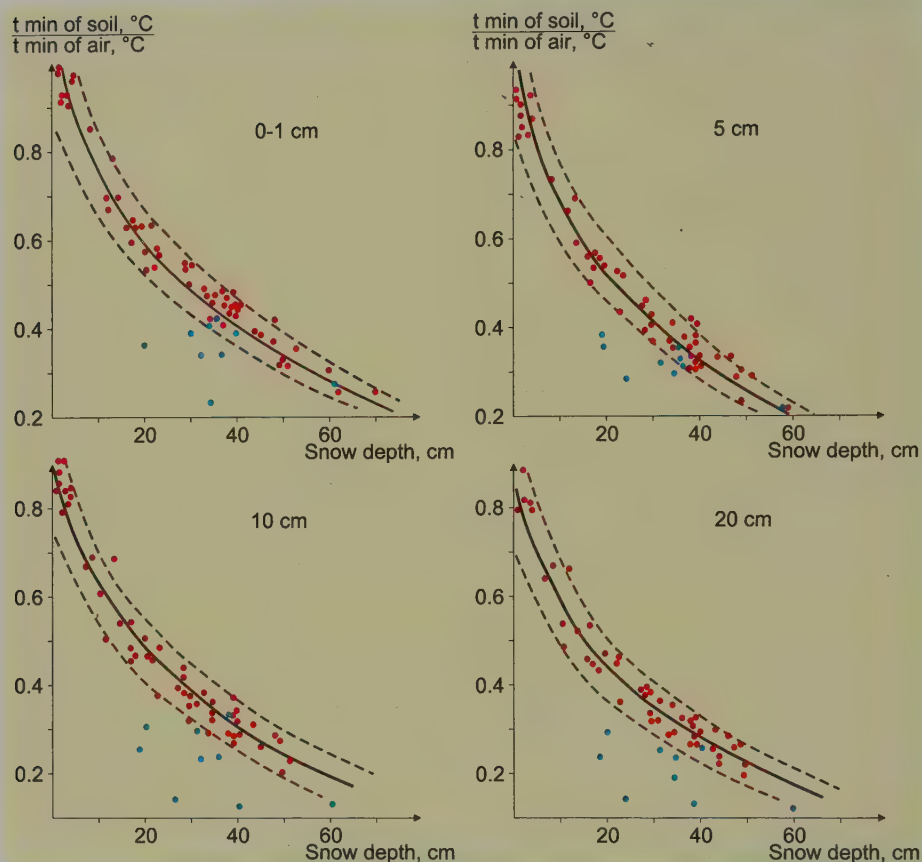
Fig. 19. Dependence of ratio between lowest soil temperature and lowest air tempera-
ture on the thickness of the snow cover in permafrost (red dots) and talik (blue dots)
biotopes. Firm line, equality of the ratio; dashed lines, 95% confidence interval.

the same snow cover thickness) increase in the lowest temperature already at
the depth of 5 cm.

SEASONAL DYNAMICS AND EXTREME TEMPERATURE
IN ANT NESTS

The temperature regime of ant nests was subject to specially detailed investiga-
tion in a sphagnum–dwarf-shrub larch forest on a train of eastern exposure. The
extreme winter temperatures of this biotope are among the coldest in the group
of biotopes with snow cover thickness 20–40 cm. At the same time, its density

of ant nests (up to 44 perm²) is among the highest (see Table 8). In addition to *Myrmica kamtschatica*, which occurs only in larch forests, this biotope contains many nests of *Leptothorax acervorum*, somewhat fewer nests of *Formica gagatoides*, and, when suitable old larch trees are present, also some nests of *C. herculeanus*. Such sparse forests occupy large areas in the region. Therefore, analysis of the temperature regime in this habitat helps to estimate both the wintering conditions in the nests of these species and the pattern of temperature courses in one of the most typical biotopes.

Temperatures were measured in the nests of *M. kamtschatica*, *F. gagatoides* and *L. acervorum* built in sphagnum tussocks. One of the *M. kamtschatica* nests (no. 1; nest numbers hereinafter refer to Table 10) was built in a sphagnum tussock in height around 25 cm and in diameter around 50 cm at the base and 30 cm at the top. Electrothermometer sensors were positioned in the surface horizon (0.5 cm) and at a depth of 5 cm at the southern, northern, western and eastern sides and at the flat top of the tussock, as well as in the moss at its centre at a depth of 15 cm. For comparison, the temperatures of a smooth part of the train without moss, and of a peat horizon (thin podbur) with sparse vegetation (cowberry, bog bilberry, Labrador tea etc.) at depths of 10, 15 and 20 cm were measured. The measurements were taken in 1978–1982 eight times per day and recorded on a logger bridge chart strip.

The most severe conditions in surface horizons of the soil over the entire period of study were recorded in the winter of 1978–1979 (Fig. 20). Average daily temperatures in the moss cover and in the mineral horizons of the soil dropped below 10 °C during the first days of September, when air temperatures dropped to 6–8 °C, and night frosts were regularly recorded. Although the surface of the soil was still warmed to 10–15 °C on sunny days, the daily range of temperatures at a depth of 10–15 cm was at most 1–2 °C in the smooth area and 3–5 °C in the moss tussock. By the day of snow cover formation (September 27), zero isotherm was established along the entire profile; only the western and the south-

Table 10. Lowest seasonal temperatures in *M. kamtschatica* nests in a sphagnum–dwarf-shrub larch forest on the train of an east-facing slope in winter 1980–1981

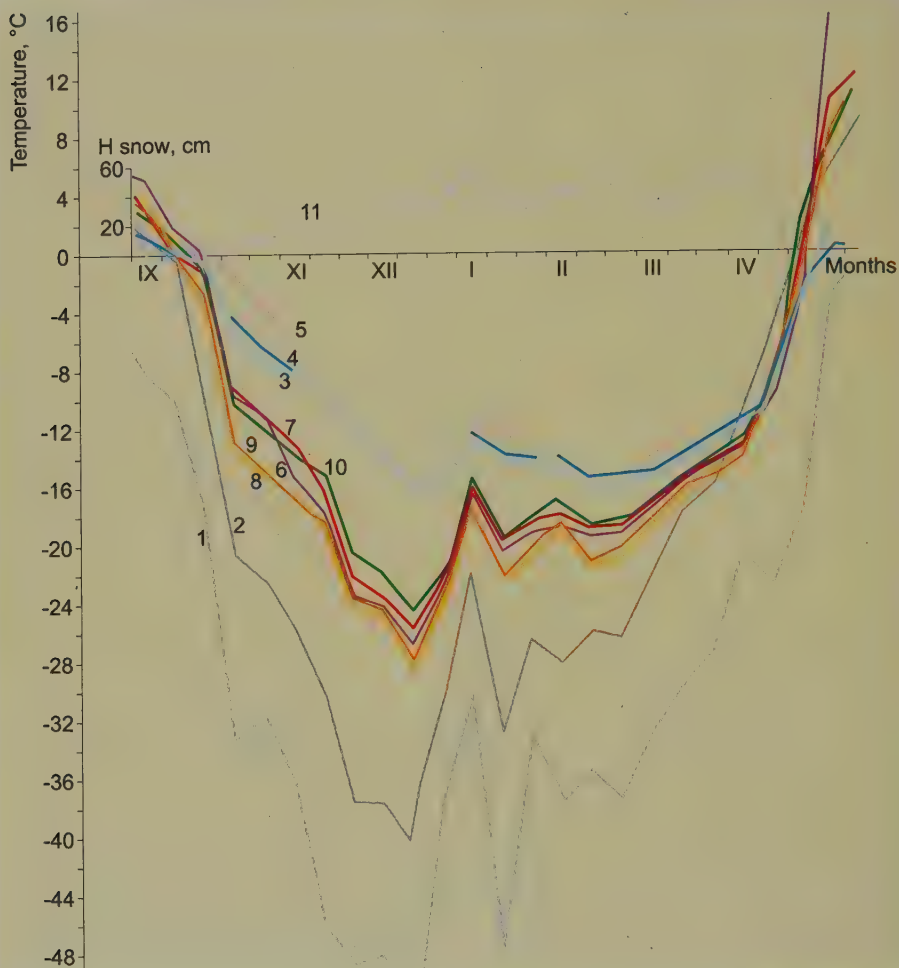| Nest no.	Lowest temperature (°C) at depth	
	15 cm	20 cm
1	−21.6	−20.8
2	−18.8	−18.2
3	−16.8	−15.7
4	−14.3	−13.4
5	−18.8	−17.7

Fig. 20. Seasonal course of air and soil temperatures and depth of snow cover in a sphagnum–dwarf-shrub larch forest on the train of an east-facing slope (500 m above sea level) in the winter of 1978–1979. Temperatures: lowest air, 1, average air, 2; 10-day average: soil, smooth area, depth 10 cm, 3; the same, 15 cm, 4; the same, 20 cm, 5; in moss tussocks, southern side, depth 0.5 cm, 6; the same, 5 cm, 7; western side, 0,5 cm, 8; the same, 5 cm, 9; centre of the tussock, 15 cm, 10; depth of snow cover, 11.

ern sides of the tussock were heated by the sun, and snow on these sides melted in the daytime (Fig. 21). Average daily air temperature varied around 0 °C from September 26 to October 9. However, it remained close to 0 °C considerably longer, until October 15, deep in the tussock (15 cm), and until October 17 in
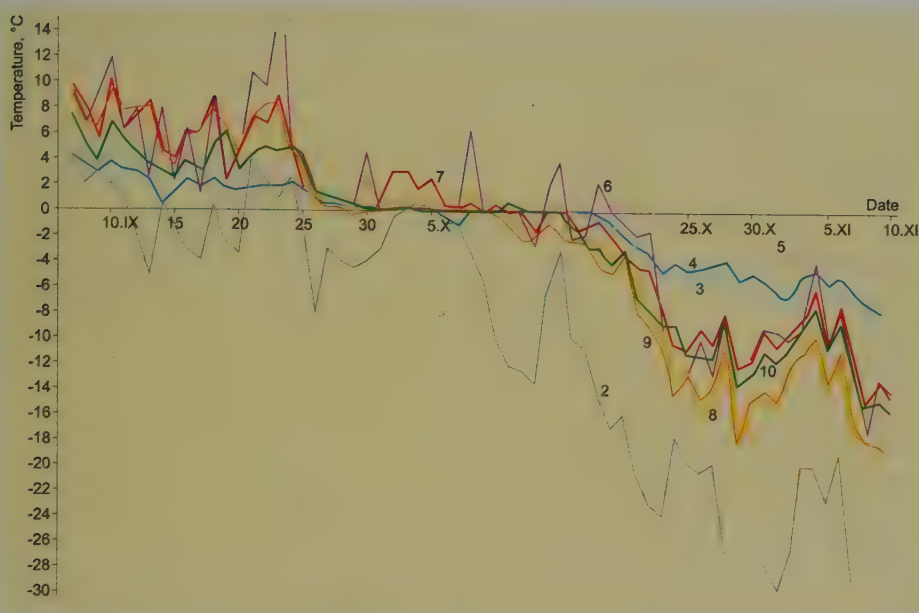
Fig. 21. Course of average daily air and soil temperatures at 3 p.m. in a sphagnum–dwarf-shrub larch forest on the train of and east-facing slope (500 m above sea level) during soil freezing in 1978; notation as in Fig. 20.

the smooth area. The longer period with temperatures around zero in the soil, compared to the air, reflected the release of the latent heat of crystallization by freezing soil water. The considerable decrease in air temperatures, which started on October 17, together with thin snow cover, resulted in quick cooling of the surface horizons of the soil: in 5–7 days the temperature in the entire tussock dropped to –12 to –16 °C and in the smooth area to –4 to –6 °C. Further cooling, even under thin snow cover, went slowly, and the range of temperatures of the soil was twice less at the upper 5 cm, and five times less at 15–20 cm than in the air (Fig. 22). The fall of air temperature in the first days of December was accompanied by a decrease in soil temperatures with the lag of 3 hours in the upper 5 cm of the tussock and 24 hours in the smooth area. The rate of cooling gradually decreased, and in the last three days before the extreme values it was 0.5 °C per day. The lowest soil temperatures were recorded on December 31, at the time of the lowest air temperatures (–54 °C) and snow cover 15 cm above the top of the tussock. The lowest soil temperature in the smooth area was –18 and –15.5 °C at depths of 10 and 20 cm, respectively, –28 to –35 °C in the upper cm of the tussock, –28 to –30.5 °C at a depth of 5 cm in the tussock, and –28 °C at a depth of 15 cm in the centre of the tussock (Fig. 23). The subsequent

Fig. 22. Course of lowest daily air and soil temperatures at 3 p.m. in a sphagnum–dwarf-shrub larch forest on the train of an east-facing slope (500 m above sea level) during the first half of the winter of 1978–1979; notation as in Fig. 20.

Fig. 23. Daily range of air and soil temperatures in a sphagnum–dwarf-shrub larch forest on the train of an east-facing slope (500 m above sea level) during the coldest period of the winter of 1978–1979; notation as in Fig. 20.

warming of the air resulted in the warming of the soil with a lag of only 3–6 hours: already after 24 hours the temperature increased by 12 °C in the upper cm, by 7 °C deep in the tussock and by 2 °C in the smooth area.

It should be noted that the coldest day of the winter of 1978–1979 was during the darkest period of the year, when the daily range of temperatures was only 2–3 °C in the air, and even close to zero in the soil (see Fig. 23). Low soil temperatures (below –10 °C) continued until April 25. In late April the snow started to melt, first on the tussock and somewhat later in the smooth area; the temperatures of the upper soil horizons increased (Fig. 24). The daily range of air temperatures during the first days of April was only 7 °C, and then increased to 15–20 °C. The daily range of soil temperatures on April 8–10 was around 1 °C at a depth of 10 cm in the smooth area, 2.5 °C at 15 cm in the tussock and 5 °C at the surface of the tussock. This parameter remained constant by April 28 in the smooth area, still covered with snow, whereas in the tussock, its top already free of snow, it increased by a factor of 2–3, to 4.5 and 15 °C at 15 cm and at the surface, respectively (Fig. 25). The fall of temperature from April

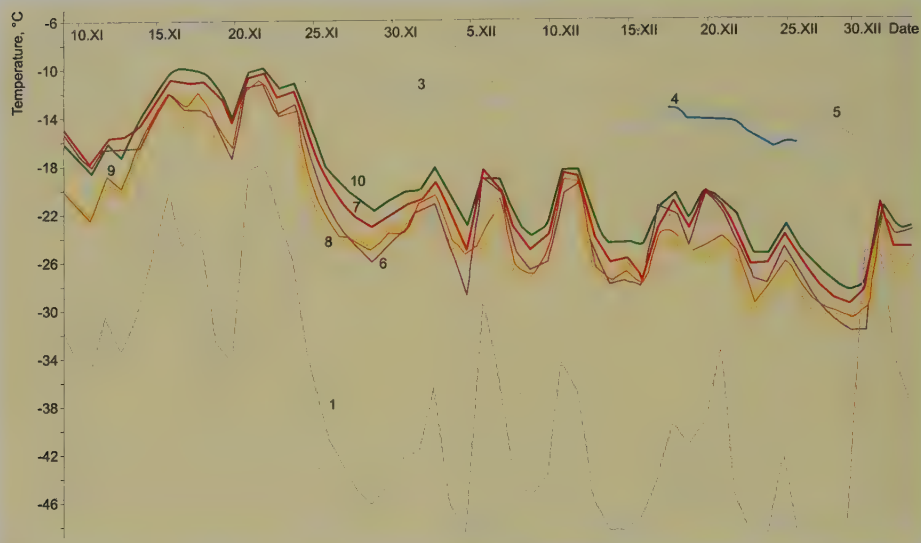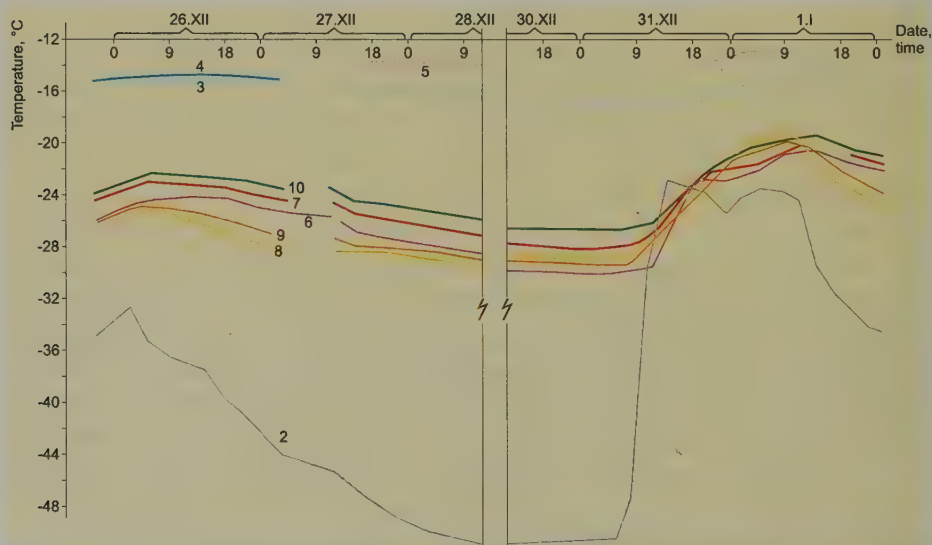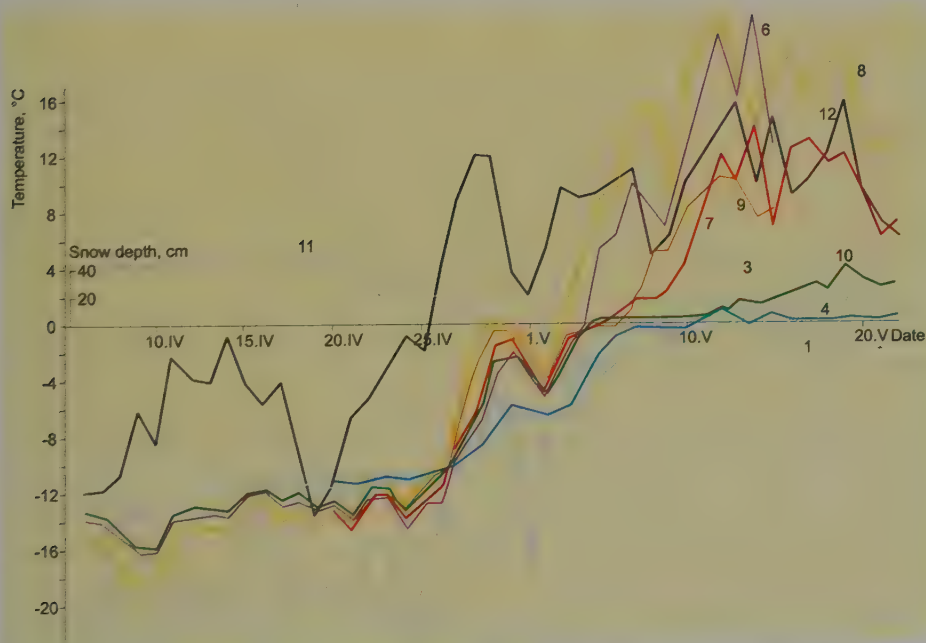**Fig. 24.** Course of the lowest and highest daily air and soil temperatures at 3 p.m. in a sphagnum–dwarf-shrub larch forest on the train of an east-facing slope (500 m above sea level) during soil thawing in the spring of 1979; highest air temperature, 12; other notation as in Fig. 20.
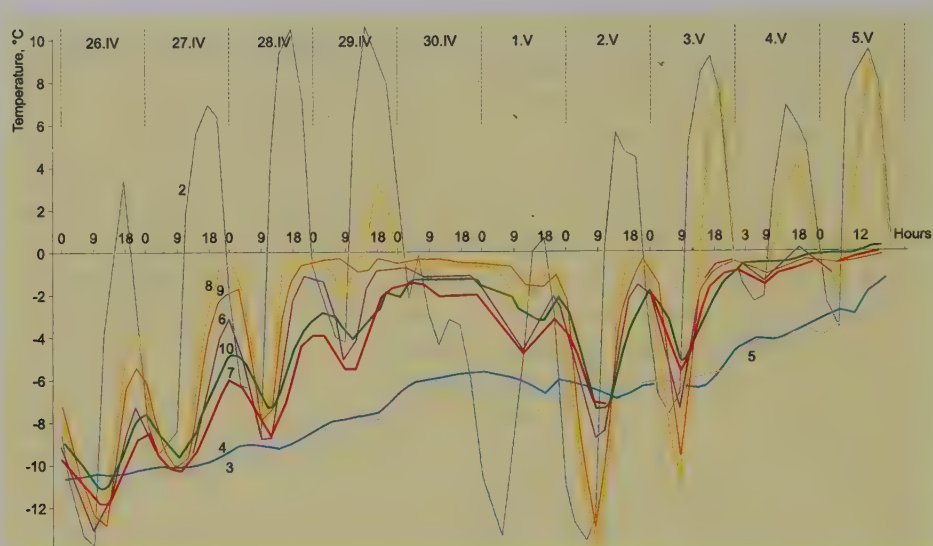
Fig. 25. Daily range of air and soil temperatures in a sphagnum–dwarf-shrub larch forest on the train of an east-facing slope (500 m above sea level) during soil thawing in the spring of 1979; notation as in Fig. 20.

30 to May 2 somewhat delayed the heating of the tussock, and the increase of temperature from −10 to 0 °C took 10 days. Thus, the spring transitional period was considerably shorter than the autumn transitional period.

The next winter (1979–1980) was the mildest over the five years of our study: air temperatures were not very low, and the snow cover was thicker (Fig. 26). Winter started almost three weeks earlier than in the previous year: sub-zero average daily temperatures were first observed on September 10–11, and became constant from September 19. Since during the last 10 days of September air temperatures were already constantly below zero, although not very low, while snow cover was still absent, the duration of the zero isotherm in the tussock was considerably shorter than in the smooth area. Freezing in the tussock reached the depth of 15 cm by September 22, i.e., temperatures close to zero were observed in this horizon for some 17 days, only 2 days less than in the previous year. Because of the snowfalls on October 10 and 20, the temperature 10 cm deep in the smooth area reached −1 °C only on October 23 and −3 °C only on November 17 (Fig. 27). The warmer last 10 days of October, compared to 1978, and the considerable thickness of the snow cover (up to 30 cm on top of the tussock and 55 cm in the smooth area) also slowed down the further cooling of the soil. The lowest temperatures in the season were observed in the tussock on January 23 at air temperature −46 °C. Their values were only −15 to −19 °C in the upper cm,
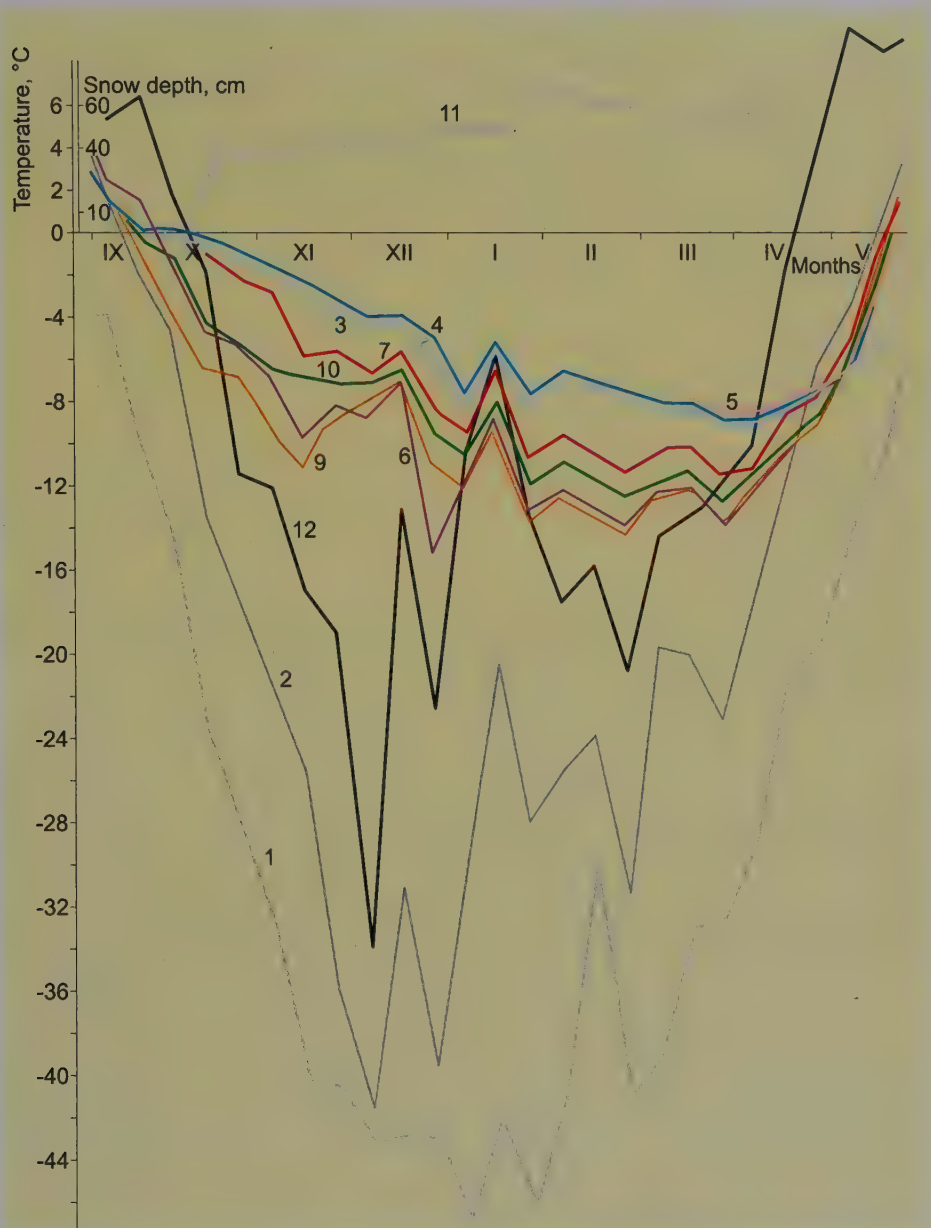
Fig. 26. Seasonal course of air and soil temperatures and depth of snow cover in a sphagnum–dwarf-shrub larch forest on the train of an east-facing slope (500 m above sea level) in the winter of 1979–1980; notation as in Figs. 20 and 24.
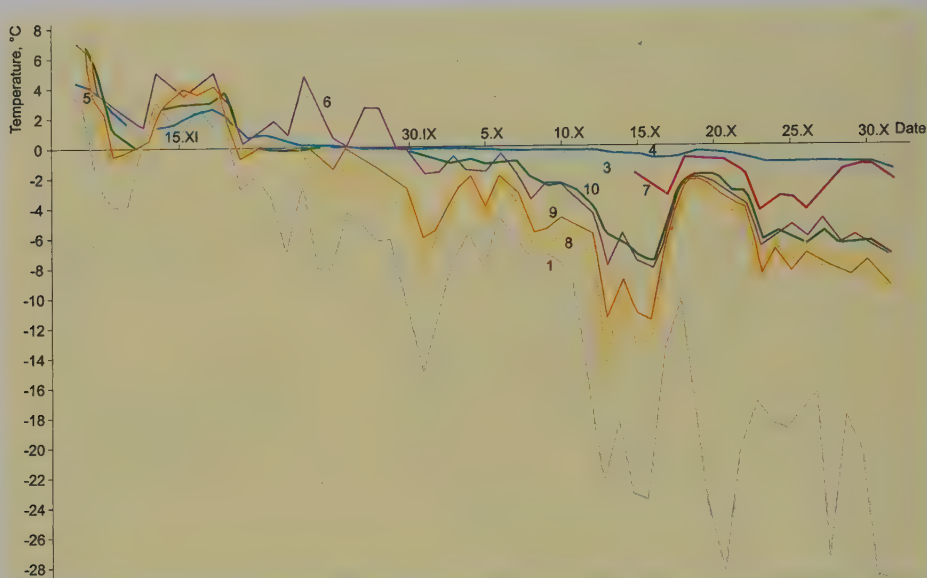
Fig. 27. Course of lowest daily air temperature and average daily soil temperature in a sphagnum–dwarf-shrub larch forest on the train of an east-facing slope (500 m above sea level), during soil freezing in 1979; notation as in Fig. 20.

–14 to –17 °C at 5 cm and –15 °C at 15 cm. Thus, the extreme values in each of the horizons were 13–15 °C higher than in the previous winter. In the smooth area the course of cooling was more even, with smaller fluctuations: the lowest temperatures were recorded only on April 1 and reached –9.7, –9.5 and –9 °C at 10, 15 and 20 cm, respectively, which is only 7–8 °C higher than in the previous winter. Thus, interannual differences in lowest soil temperatures were greater in tussocks than in smooth areas, because of the thicker snow cover of the latter.

The rate of soil temperature increase was high, as in the previous year: the temperature of each horizon rose from –6 to –7 to 0 to –1 °C from May 8 to May 13, but further thawing took nine more days in the upper horizons of the tussock and at least two weeks deep in the tussock and in the smooth area (see Fig. 26). The total duration of sub-zero temperatures was 7.5 months, i.e. 2–3 weeks longer than in the previous winter.

In addition to interannual fluctuations, we estimated the unevenness of the temperature field over a large area, to find out to what degree the microclimatic differences we observed between two adjacent elements of the nanorelief (tussock vs. smooth area) were representative of the whole biotope. The above-discussed part of the sphagnum–dwarf-shrub larch forest was a good example

in this respect as well, since it had pronounced nanorelief (tussocks in the shape of pillows) and uneven snow cover, reflecting the nanorelief, and mosaic pattern of the vegetation. The temperatures on the surface of 10 sphagnum "pillow" tussocks 20 cm high were 10–13 °C lower than the temperatures in the lower areas between them, measured simultaneously in December 1978: −25 to −30° and −17 to −21 °C, respectively, at air temperature −48 °C and thickness of the snow cover 12–15 cm on top of the tussock and up to 35 cm in the lower areas. In other words, patterns similar to the one described above by the example of two adjacent elements of the nanorelief are typical of the entire biotope.

The range of temperatures in the soil of different elements of the nanorelief of a sphagnum–dwarf-shrub larch forest we described in the winters of 1978–1979 and 1979–1980 did not change in later years. Measurements taken in the winter of 1980–1981 in several nests of *M. kamtschatica* in the same area showed that the lowest seasonal temperatures were reached twice, on February 26 and on March 2; between these days the temperatures increased by 1–2 °C. Even in the coldest of the studied nests (no. 1, Table 10) the lowest temperatures were 8–10 °C higher than at the same depth in 1978—1979, whereas the temperature in the warmest nests was 12–14 °C higher.

These data on the daily range and seasonal course of temperatures, including their extreme values, and on their interannual and spatial variation in surface horizons of different elements of the nanorelief show that the more dramatic fluctuations of temperatures in the tussocks, compared to smooth areas, are a characteristic feature of the thermal regime of the soils in a sphagnum–dwarf-shrub larch forest. The same is true of the overwintering conditions of several ant species.

M. kamtschatica is found exclusively in the above-described type of biotopes, therefore these data fully characterise the wintering conditions of this species, which can be briefly described as follows. In areas with winter duration 7.5 months the temperature in overwintering chambers at a depth of 15–20 cm remains in some years below −10 °C for over 5 moths, below −15 °C for over 3 months, and below −20 °C for over 1 month. The lowest temperature in the nest varies within the biotope depending on the height of tussocks, and from year to year depending on the seasonal courses in snow cover thickness and air temperatures, reaching usually −14 to −21 °C, and −26 to −28 °C in the most unfavourable seasons.

F. gagatoides, like *M. kamtschatica*, builds its nests in sphagnum–dwarf-shrub larch forests in moss tussocks, where it overwinters at depths of 10–20 cm, preferably in areas with less developed nanorelief. The temperatures in a *F. gagatoides* nest were measured daily in a larch forest of this type on the train of a south-facing slope in the winter of 1976–1977. The courses of temperatures averaged for each five days (Fig. 28) differs from the above-described courses of *M. kamtschatica* only in the longer period with temperatures close to 0 °C. The
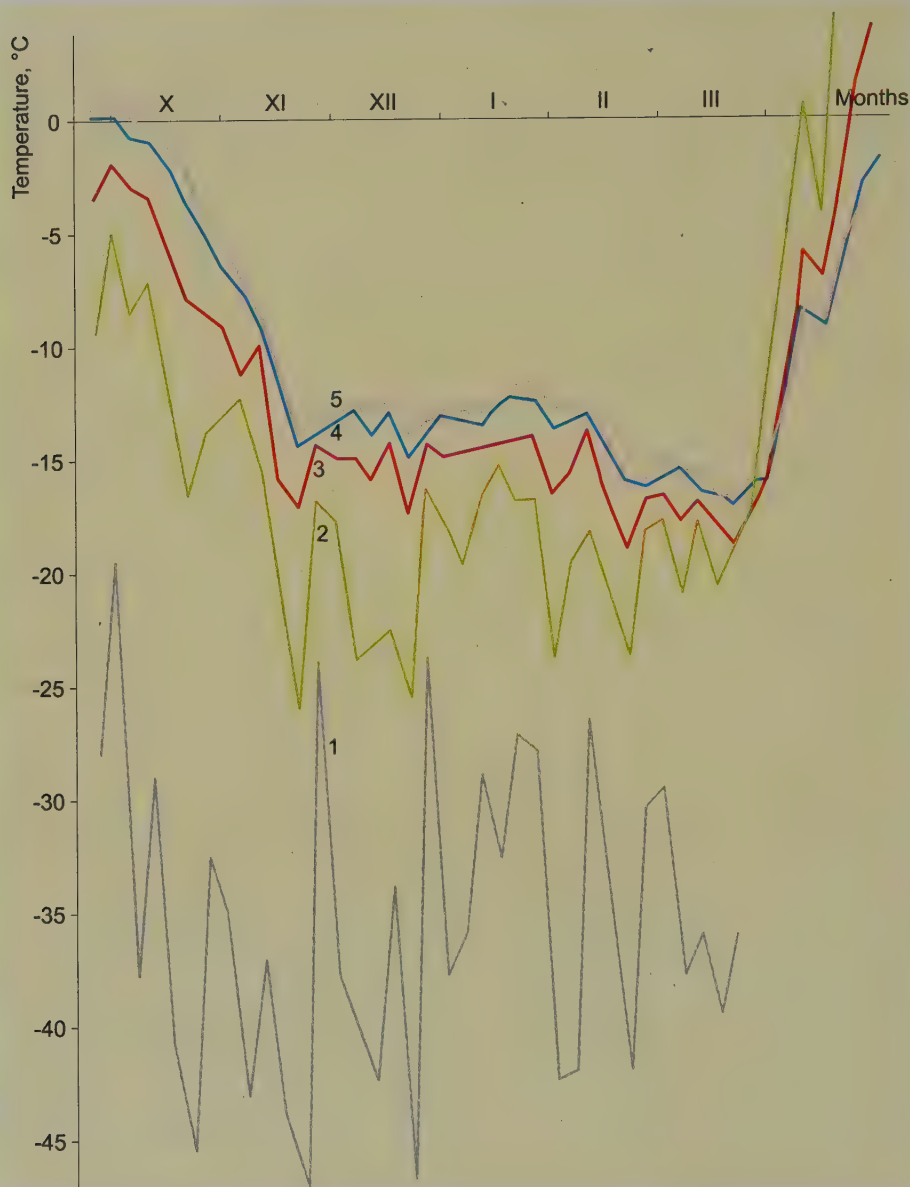
Fig. 28. Seasonal course of temperature in the overwintering chambers of a *F. gagtoides* nest in a sphagnum–dwarf-shrub larch forest on the train of an east-facing slope (500 m above sea level) in the winter of 1976–1977. Averaged 5-day temperature at 3 p.m.: air, 1; soil surface, 2; soil at the depth of 5 cm, 3; soil, 15 cm, 4; soil, 20 cm, 5.

lowest values were recorded in late March in all the horizons, except the surface, where equally low values (−26 °C) were recorded twice: in late November and in late December. The temperature reached −19 °C at a depth of 5 cm, −17.4 °C at 10 cm and −17.2 °C at 20 cm, which is close to the lowest values observed in the coldest nests of the preceding species.

During the winter of 1980–1981, temperatures were measured in four nests of *F. gagatoides* (nos. 6, 7, 8, 9) built in the part of the train of the east-facing slope repeatedly mentioned above in two nests (nos. 10, 11), in a xerophyte meadow community of a dry rubbly area in the lower part of a south-facing slope (surface cover of cowberry, pasque flower and dog rose), and in two nests (nos. 12, 13) in a larch forest with willow undergrowth on a terrace of the Olen Brook (Table 11). The last two areas both have medium snow cover thickness, but the south-facing slope is one of the cold areas and the brook terrace is one of warmest (see Table 9, areas no. 14 and 41). Thus, measurements taken in four markedly different areas give us a relatively thorough picture of the range of overwintering conditions in the nests of *F. gagatoides*. The lowest temperatures in the overwintering chambers of its nests are only −10 to −12 °C in the warmest areas and −15 to −20 °C in most of the study area. The lowest temperatures are found in nests built in sphagnum tussocks and on dry rubbly areas with medium snow cover thickness. The lowest temperatures recorded in such nests reached −20 °C; in more severe winters they can probably reach −23 to −25 °C.

L. acervorum is least protected from cold in the course of overwintering, which is shown by the results of measurements taken in some years in 8 nests built in the soil in markedly different habitats. The lowest temperatures were found in nests built in moss tussocks, where, as noted above, the temperatures

Table 11. Lowest temperatures in *F. gagatoides* nests in winter 1980–1981 in different typical biotopes of this species (for descriptions, see text)

Area	Nest no.	Date when lowest value was recorded	Lowest temperature (°C) at depth (cm)				
			0	5	10	15	20
Train of east-facing slope	6	2.III.1981	–	–	–	−16.8	−153
	7	2.III.1981	–	–	–	−18.8	−17.7
	8	2.III.1981	–	–	–	−15.4	−13.5
	9	2.III.1981	−26.0	−19.0	−17.4	–	−172
South-facing slope	10	3.I.1981	–	−19.1	−17.5	–	−16.7
	11	3.I.1981	–	−20.1	−19.7	–	−17.8
Terrace of Olen Brook	12	2.III.1981	–	–	−19.7	–	–
	13	2.III.1981	−19.0	–	−11.6	–	−10.8

Note. "–", no data.

sometimes reach −28 to −30 °C (see Fig. 20). The temperature at 5 cm can be lower only in biotopes with the thinnest snow cover; the soils of areas covered with snow are usually warmer at this depth (see Table 9, Fig. 17). Thus, the range of the lowest winter temperatures in the nests of *L. acervorum* is not much narrower than the entire range of the lowest soil temperatures at a depth of 5 cm.

C. herculeanus overwinters in conditions no milder than the preceding species. The lowest temperatures in the overwintering chambers positioned in fallen trees at the surface of the soil or in roots at the depth of around 5–10 cm sometimes reach −25 to −26 °C (Fig. 29). In the winter of 1980–1981 the lowest temperatures in a nest positioned in the lower side of a large fallen larch trunk, almost not covered with soil, were −25 °C, due to the considerable amount of wood, which is only 5 °C lower than the temperature recorded at the same time in the roots of a stump at a depth of 5 cm from the surface. In other words, the regime in the overwintering chambers of *C. herculeanus* built at the base of stumps or in tree trunks half-buried in soil differs little from the regime of corresponding horizons of the soil. The principal peculiar features of this regime are
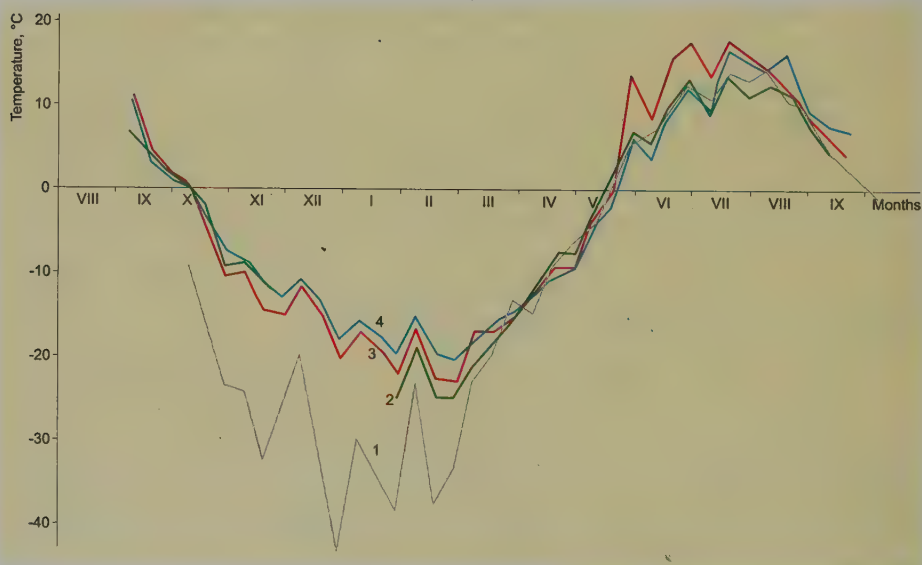
Fig. 29. Seasonal course of 10-day averaged temperatures at 3 p.m. in the wintering chambers of *C. herculeanus* nests and average daily air temperatures in a dry dwarf-shrub–lichen larch forest on the terrace of the Olen Brook (500 m above sea level) in the winter of 1977–1978. Temperatures: air, 1; in the overwintering chambers of *C. herculeanus* nests in the lower part of a larch stump (25 cm in diameter), 2; in a fallen larch trunk, 3; and in the soil under the fallen larch trunk at the depth of 15 cm, 4.

probably only the short period with temperatures close to zero in autumn and the rapid warming in spring after the melting of the snow.

L. muscorum is subject to the action of still lower winter temperatures than the two preceding species. In the Oymyakon depression, with very severe frosts and relatively thin snow cover, the upper horizons of the soil are strongly cooled. Unfortunately, we were unable to compare the results of our measurements taken in the soil every 5–7 days in the winter of 1977–1978 on a steppe slope in the valley of the Uchugey River with continually recorded data from any

Fig. 30. Seasonal course of air and soil temperatures and depth of snow on a steppe slope of the valley of the Uchugey River (tributary of Agayakan River; 3 km from the mouth) in the winter of 1977–1978. Temperatures: air at Agay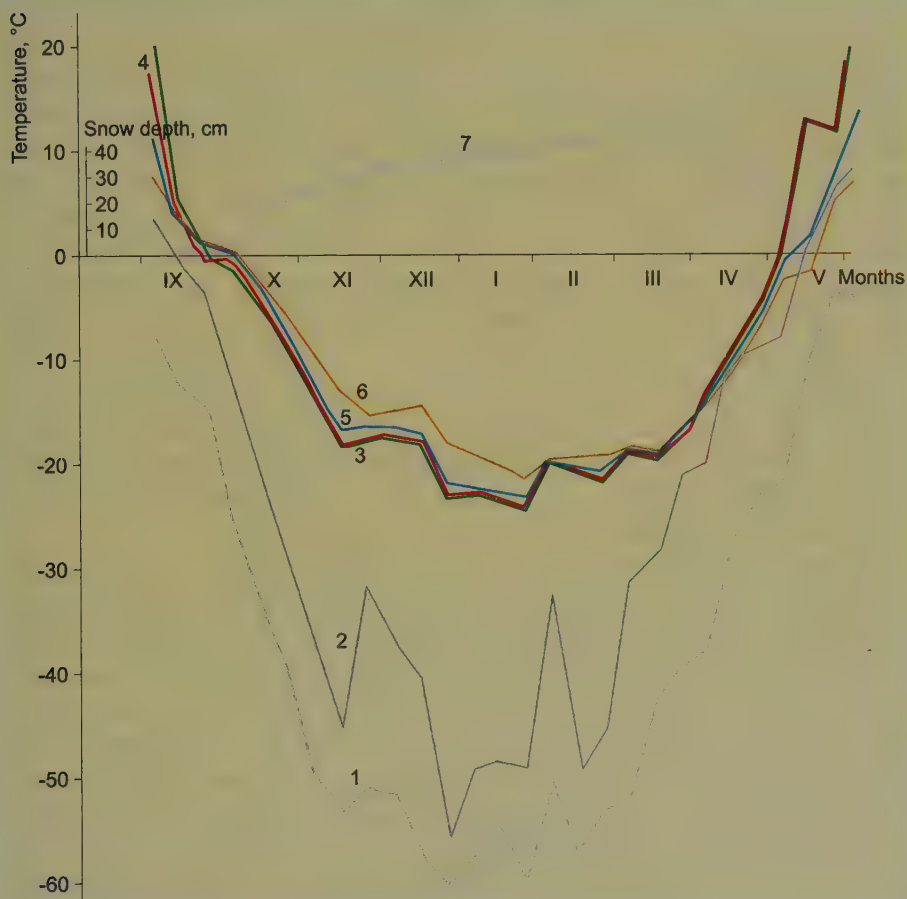akan Meteorological Station: absolute minimum over ten days, 1; 10-day average, 2; soil temperatures, measured once a day at the depth of 1 cm, 3; 5 cm, 4; 15 cm, 5; 40 cm, 6; snow cover depth, 7.

adjacent biotope, as we did in the environs of the Aborigen Station (Fig. 30). However, the figure shows that a considerable number of measurements were taken on days with air temperatures close to the lowest seasonal value. Thus, it is probably safe to consider also the recorded lowest temperatures in the soil close to the true lowest values.

The lowest air temperature (−59.8 °C) was recorded in the second 10 days of December, and the lowest soil temperatures were recorded in late January. With the average daily temperature −56.7 °C and the snow cover thickness 37 cm, the lowest temperatures in the soil were −25 °C at a depth of 1 cm, −24.7 °C at 5 cm, −23.7 °C at 15 cm, −22.8 °C at 20 cm, −21.0 °C at 40 cm. The difference between temperatures at the depths of 1 and 40 cm was as small as 4 °C, and between 1 and 15 cm it was only 1.3 °C. Thus, estimating wintering conditions, we can safely ignore the differences between the depths at which overwintering chambers are positioned. Taking into account the fact that winter air temperatures at the Oymyakon Meteorological Station are 1.5–2.5 °C lower than at the Agayakan Meteorological Station, and the fact that in the year of our study on the steppe slope where our measurements were taken the snow cover thickness was considerably greater than the annual average (Spravochnik…, 1966), we can suppose that the winter temperatures in the nests of *L. muscorum* can be lower than those we recorded.

In total, ants were exposed to negative temperatures in the winter of 1977–1978 for 7 months, to temperatures as low as −10 °C and lower for 5.5 months, below −15 °C for 4.5 months, and below −20 °C for two months. Thus, the overwintering conditions of *L. muscorum*, a species overwintering in the soil under snow, can be considered quite severe.

M. bicolor and *F. candida*, as noted in Chapter 2, colonize floodplain terraces, often in the immediate proximity of each other. Thus, the measurements taken in the floodplain of the Detrin River at the edge of a poplar-chosenia forest near a nest of *M. bicolor* can be applied to both species. As mentioned above, poplar-chosenia forests are connected in their distribution to the talik zones of river floodplains, where their existence is facilitated by the special hydrothermal regime. However, the winter temperature regime of the sand-pebble alluvium in the area where ant nests were found, at least to the depth of 60 cm, differed little from the conditions in the soils of permafrost biotopes outside the floodplain. The alluvium was frozen at the beginning of winter simultaneously with soils outside the floodplain. At the end of January the temperature of the pebble ground reached −17 °C in the upper cm, −15 °C at 5 and 10 cm, and varied from −9 to −12.5 °C in the layer where overwintering chambers were positioned, at a depth of 30–40 cm (Fig. 31). Later the temperature decreased to −20 °C at 20 cm. Thus, the overwintering conditions in the area where the ants build their
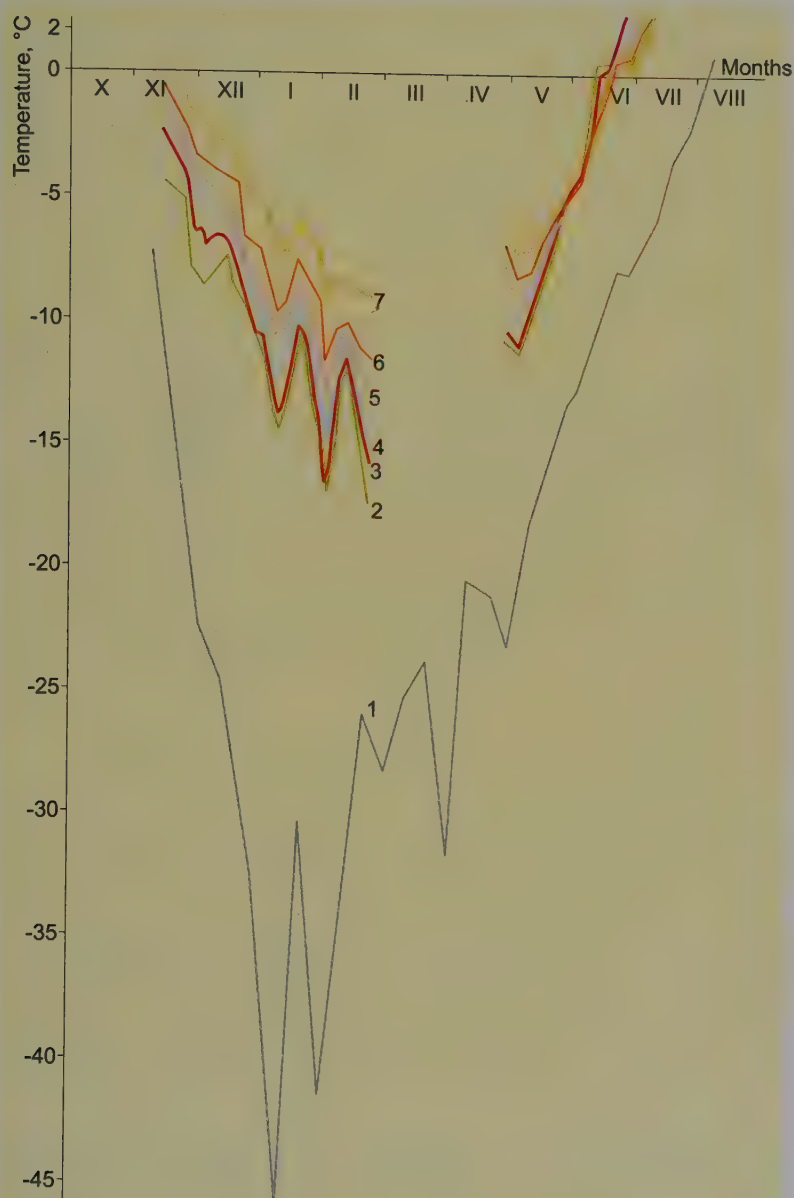
Fig. 31. Seasonal course of air and soil temperatures at the edge of a poplar-chosenia grove in the floodplain of the Detrin River near a nest of *Myrmica bicolor* (480 m above sea level) in the winter of 1979–1980. Temperatures: air (10-day average), 1; soil (measured once in every 4 days) at the surface, 2; at the depth of 5 cm, 3; 10 cm, 4; 20 cm, 5; 40 cm, 6, 60 cm, 7.

nests were no milder than in most permafrost biotopes of the sparse forest belt. The specific thermal regime of the talik zones is probably apparent here only in spring, when the relatively thin layer of frozen ground thaws both from above (by insolation and warm air advection) and from below (by the heat of the river water). However, the thawing of the ground from below makes the overwintering period of ants only slightly shorter. The difference between the river talik and dry rubbly areas with permafrost in the time of thawing to the depth where overwintering chambers are built (40 cm) is at most 10–15 days, i.e. 5-10% of the period of seasonal activity of ants (Alfimov, 1985).

F. exsecta, as noted above, sporadically occurs in various habitats, and the distribution of this species does not reflect specific ecological conditions of the warm season. Therefore we paid special attention to revealing the winter temperature regime in its nests. In different years, temperatures were measured in nine nests of *F. exsecta* in different areas (three of these nests were studied over 3–4 years).

To determine the impact of the piled-up cone on the temperature regime in the nests of *F. exsecta* in winter, two series of electrothermometers where installed in three nests: directly in the chambers of the nest and at a distance of 0.6–1 m from the cone in corresponding horizons of the soil. It was found that the temperatures under the cone, about half a metre high and 60 cm in diameter at the base, and in the soil near the cone were equal, so the cone has no heat-insulating effect in winter.

The lowest temperatures in the nests of *F. exsecta* in different areas were virtually the same, in spite of the considerable differences of the areas in altitude, relief, vegetation, soils, groundwater level and thickness of the seasonally thawed layer and of the snow (Fig. 32). In the layer where most ants overwinter, the lowest temperatures fall within the range −9 to −12 °C. The depth of the position of this layer, as is clear from Fig. 32, varies from 120 cm on a sandy terrace of the Kolyma to 5 cm in the depression of Jack London Lake. The sandy ground of the terrace and the levees of the Kolyma, with snow cover thickness 40–50 cm and very low air temperatures, is cooled to −16 °C at 20 cm, while ants overwinter considerably deeper, where the temperature remains rather high (already at 60 cm it is never lower than −12 °C). In the depression of Jack London Lake values close to the lowest temperature are observed at a depth of only 5–10 cm, due to the thick (up to 80 cm) and loose snow cover, as well as by the higher values of the lowest air temperatures, which in this area are 8–10 °C greater than in the Kolyma valley. The same factors (air temperature and snow cover) determine the high temperatures in nests built on south-facing slopes (which are, at the same time, leeward) in mountain tundras and sparse forests at 750 m above sea level. In mountain tundras with the lowest air temperature reaching no lower than −37 to −40 °C, wind-accumulated snow (70–80 cm) maintains in the upper
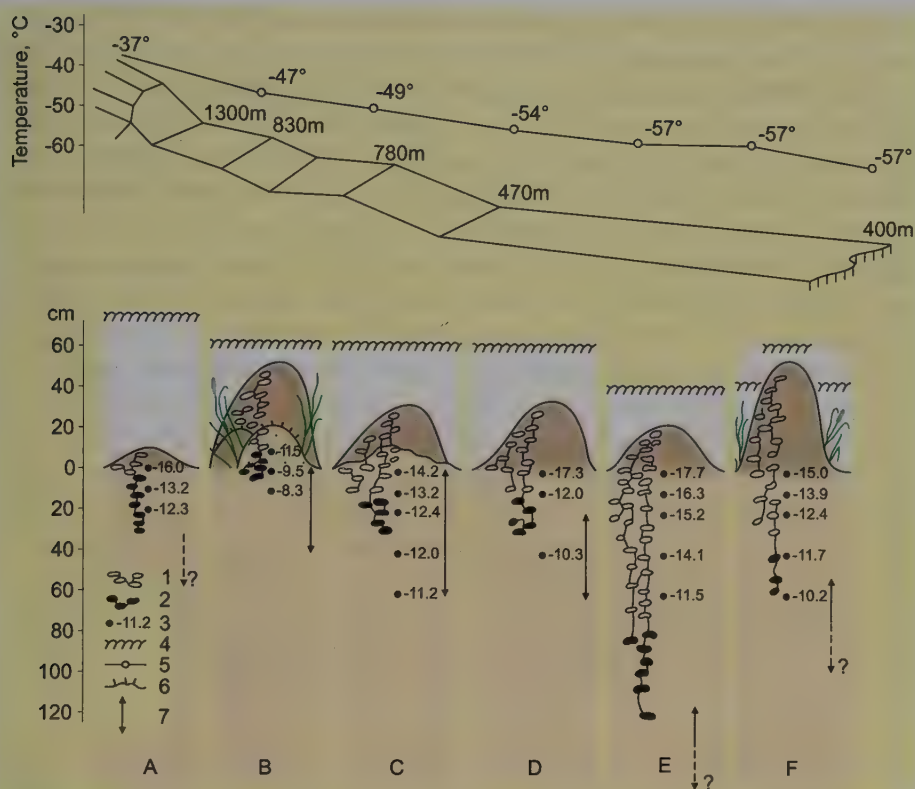
Fig. 32. Position of the overwintering chambers and lowest temperatures in *F. exsecta* nests in different habitats: A, south-facing slope in mountain tundra; B, depression of Jack London Lake; C, trains of slopes along the Olen Brook; D, talik zone of a terrace of the Olen Brook; E, sand deposits on a terrace of the Kolyma; F, levee of the Kolyma. Key: 1, summer chambers; 2, overwintering chambers; 3, location of electrothermometers and lowest winter temperatures; 4, snow cover depth; 5, absolute air minimum; 6, surface of a tussock buried under an anthill; 7, lowest and highest levels of underground waters during the season (dashed line and question mark, lowest level not determined).

horizons of the soil relatively high temperatures: no lower than −12 to −13 °C at a depth of 20 cm. In larch forests at 750 m above sea level the same effect is achieved by the 7–8 °C increase in air temperatures and by the 10–15% increase in the snow cover thickness, compared to the bottoms of valleys. However, ant nests in these biotopes are usually built in shallow erosional depressions, which are filled with snow even in the years with little snowfall.

Favourable conditions in the nests of *F. exsecta* may also result from the warming effect of groundwaters. The presence of groundwaters is usually in-

dicated by wintertime formation of aufeis, the thickness of which in our study area varies by spring from 20–30 cm to 1.5 m, and in some places even to 2.5 m. It is the influence of groundwaters, together with loose snow cover, that helps preserve high temperatures in the nests we examined in larch forests on the terraces of the brooks Olen and Ozyorny. The duration of the period with temperatures close to zero in the nests of *F. exsecta*, as in the nests of *M. kamtschatica*, *F. gagatoides* and *L. acervorum*, found in the sphagnum–dwarf-shrub larch forest described here in detail, depended on the course of air temperatures and snow cover thickness and considerably varied from year to year. For instance, the temperature at a depth of 10 cm remained within the range +1.5 to 0 °C for two weeks in the autumn of 1978 (Fig. 33), and for over two months in the au-
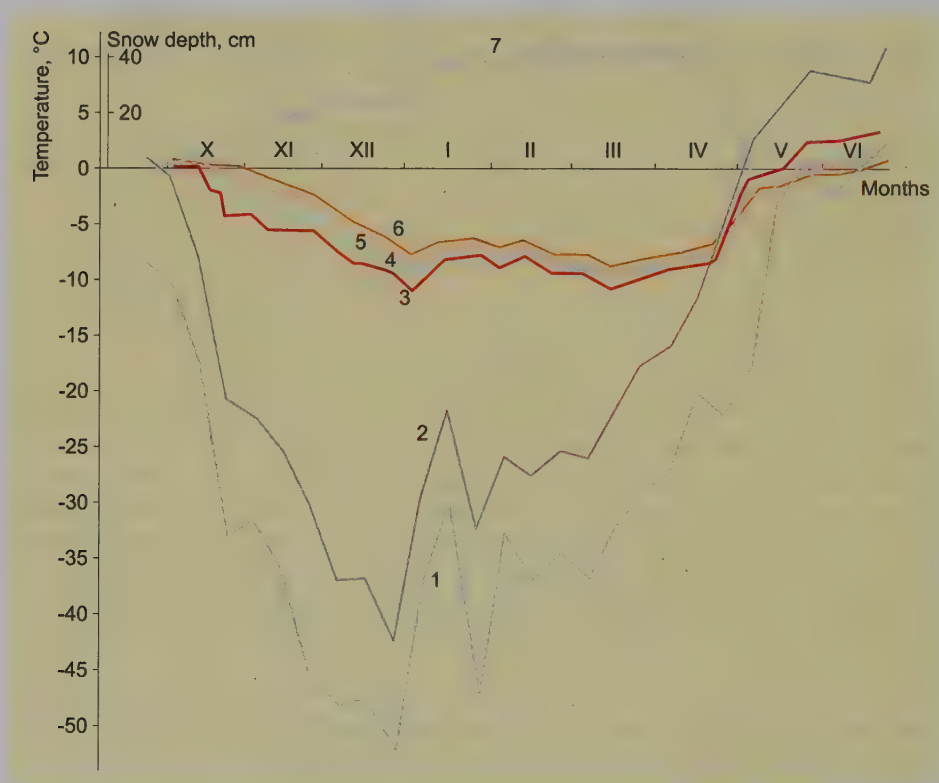
Fig. 33. Seasonal course of air temperatures, temperatures in the wintering chambers of a *F. exsecta* nest and snow cover depth in a herb–dwarf-shrub larch forest with willow undergrowth on a terrace of the Olen Brook (480 m above sea level) in the winter of 1978–1979. Air temperatures: 10-day lowest, 1; 10-day average, 2. Temperatures in the nest: at the depth of 5 cm, 3; 10 cm, 4; 20 cm, 5; 40 cm, 6 (measured once in every 5–7 days). Snow cover depth, 7.

tumn of 1979 (at 40 cm it remained within this range for one and two months, respectively). It should be noted that ants are no longer seen on the surface of the dome from the first days of September (and sometimes even earlier), but continue moving in deep tunnels until the end of October, at only slightly sub-zero temperatures. Such movements were first described in the nests of *F. rufa* (Marikovsky, 1965), and later in *F. polyctena* (Seima, 1998).

The subsequent cooling of the surface horizons is also slow, and soil temperatures remain relatively high during the first half of winter even at very low air temperatures (−45 to −55 °C) and the snow cover still rather thin. The lowest soil temperatures are observed from January to late March.

F. sanguinea was found only in two larch forests on the terraces of the brooks Ozerny and Olen, where this species coexists with *F. exsecta*. Thus, the temperature conditions in the nests of *F. exsecta* and *F. sanguinea* can be considered close, if not identical. In other words, the temperature regime of *F. sanguinea* nests is similar to that shown in Fig. 33 both in temperature courses and in lowest temperatures in wintering chambers.

F. lemani colonizes quickly and deeply thawing areas of south-facing slopes; shafts of this species go into the soil deeper than 150 cm. A general outline of the temperature regime of the surface horizons in *F. lemani* habitats
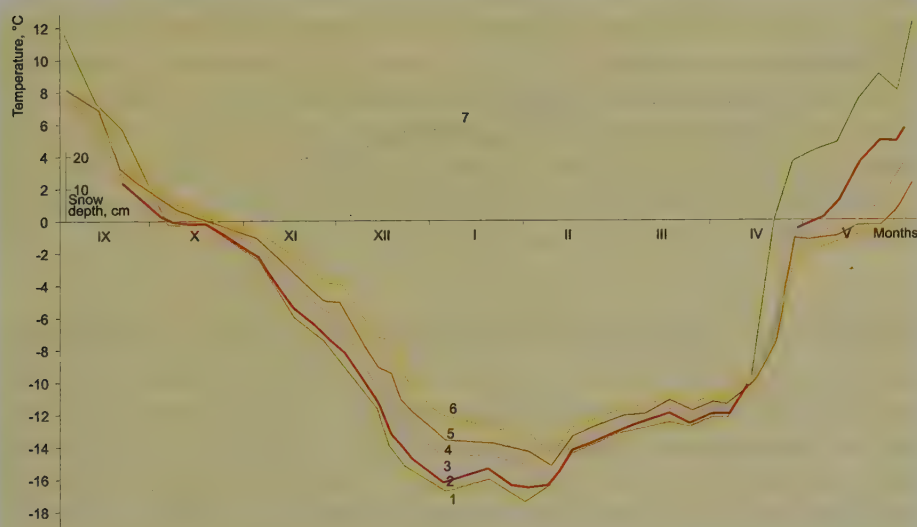

Fig. 34. Seasonal course of soil temperature and snow cover depth in a sparse larch forest on a south-facing slope in the winter of 1981–1982. Temperatures of the soil: at the depth of 1 cm, 1; 5 cm, 2; 10 cm, 3; 20 cm, 4; 40 cm, 5; 60 cm, 6 (measured once in every 5–7 days). Snow cover depth, 7.

is shown in Fig. 34. The upper inhabited horizon is subject to considerable interannual temperature fluctuations, resulting from differences in air temperature and snow accumulation courses, as well as from the relatively low heat capacity of the soil, which in late autumn has water content at most 10%. In addition, in these favourably exposed biotopes snow sometimes melts completely during autumn thaws, and subsequent decreases in air temperatures have especially strong impact on soil temperatures. The range of lowest annual temperatures in the upper cm of the soil over several years of study in a larch forest and an aspen forest (with mesoxerophyte cover) on a south-facing slope was around 10 °C (−17 to −27 °C and −13 to −23 °C, respectively), i.e. around one third of the entire range of lowest temperatures observed in the region. However, already at the depth of 20 cm the variance decreased to 4–5 °C. A still wider range of lowest winter temperatures of the soil was found in the set of all the studied areas inhabited by *F. lemani*: −13 to −26.5 °C in the upper cm, −10 to −20 °C at 20 cm, −8 to −19 °C at 60 cm, and from −5 to around −16 to −17 °C at 80 cm. Such considerable variance of temperature conditions in areas similar in vegetation type, humidity and soil texture is determined mostly by differences in snow cover thickness, which, in its turn, depends on the microrelief and the position of the area regarding the direction of prevalent winds. It follows from all these data that we may consider −12 to −15 °C the normal range of lowest seasonal temperatures in the overwintering chambers of this species, positioned at depths no less than 50–60 cm. Such temperatures are observed at a depth of 60 cm in most of the study area. However, these horizons are suitable for overwintering of ants only on slopes of southern exposure and, above all, low water content, since in most of the studied biotopes the layer 50–60 cm deep thaws only in late summer, whereas on dry southern rubbly slopes the temperature at 50–60 cm rises above 0 °C in the middle or in the second half of May.

RANGES OF LOWEST TEMPERATURES IN SOILS AND IN ANT NESTS

Summarizing all the above-given information on the temperatures of the upper soil horizons and on the overwintering conditions of ants, let us emphasize the most important points. The position of the region in the zone of continuous permafrost and the proximity of the Northern Hemisphere's Pole of Cold determine the peculiar features of the hydrothermal regime in the upper soil horizons. The low rate of thawing in most of the area leaves only the upper horizons of the soil, thawing by the end of June to a depth of 25–30 cm, suitable for the life (including overwintering) of ants. An exception to this rule is the rare areas

where the ground thaws quickly and deeply (over 1–1.5 m); ants colonizing such areas are consequently able to winter at considerable depth.

The range of the temperature distribution of the study area is extremely wide and virtually continuous. Biotopes differing in snow cover thickness, type of vegetation, soil water content etc. form a continuous sequence with temperatures in the upper 20 cm of the soil changing from −48 to −10 °C along the vertical profile from the bank of the Kolyma to the upper boundary of mountain tundras.

The lowest soil temperatures (−36 to −48 °C in the upper cm and −29 to −39 °C at 20 cm) were recorded only in a few areas of the sparse forest belt; the greatest seasonal thickness of the snow cover in these areas seldom reaches more than 10 cm. In mountain tundras the range of lowest soil temperatures of the same horizons is −34 to −38 and −32 to −34 °C, respectively. In most of the Upper Kolyma region, snow cover 20–40 cm thick prevents cooling below −28 to −30 °C in the upper cm of soil and below −20 to −24 °C at 20 cm. Still greater thickness of the snow cover almost invariably keeps the temperatures of these horizons no lower than −25 and −17 °C, respectively, even at lowest air temperatures close to −60 °C.

The highest values of lowest temperatures (around −10 to −13 °C in the layer 10–40 cm deep) are observed in a small number of habitats. In the sparse forest belt these include either talik zones, or areas near the tree line with thick snow cover (lake depressions, brook valleys, erosional depressions, leeward slopes), or some other biotopes with thick snow cover (due to favourable combinations of exposure, microrelief and vegetation) and high soil water content. The surface layers of talik zones in cases of deep water-bearing horizons can cool to the same degree as the soils of normal permafrost biotopes. In the mountain tundra belt high temperatures in the upper soil horizons are retained only under accumulations of snowdrifts of considerable (over 70–90 cm) thickness; the area of such localities is rather small.

An important feature of the temperature regime of permafrost soils is the autumn transitional period with temperatures close to zero along the entire profile except the upper 3–5 cm. The duration of zero isothermy fluctuates from 1–2 weeks in dry areas in years of late snow cover formation to 1.5–2 months in humid areas, especially in years with early and intensive snowfall covering non-frozen earth.

The courses of soil temperatures are fairly smooth in most biotopes (except dry and snowless ones). It is extremely important that abrupt and large falls of air temperature are reflected in the soil as smooth falls with considerable lag, due to the heat-insulating effect of the snow cover and the high heat capacity of soils, especially very icy ones. Daily ranges of soil temperature at depths greater

than 5–10 cm even under relatively thin snow cover are virtually absent in the middle of winter. Thus, overwintering ants are in most cases protected both from very low temperature (recorded above the surface of the snow) and from its abrupt fluctuations.

Because of this lag effect, lowest soil temperatures are endured by overwintering ants for at least 24 hours and higher temperatures (1–3°C higher than minimum) for 1–2 weeks to several months. In such conditions the success of overwintering is determined by the value of the lowest temperature and depends little on its duration (see below).

The duration of winter—the period between the days when stable below zero and stable above zero temperatures are established—differs little in the layer of soil inhabited by ants in different areas and amounts usually to 7–7.5 months; on dry areas of south-facing slopes it is 3–4 weeks shorter.

The overwintering chambers of the studied ant species were found in the following temperature ranges against the above-described background.

F. exsecta was found, on the one hand, in habitats with highest values of lowest soil temperature (in biotopes with thick snow cover and in talik zones of large brooks) and, on the other hand, in the rare deeply thawing areas (levee and sandy terrace of the Kolyma), where the overwintering chambers were positioned at abnormally great depth (80–120 cm), compared to the background. Overwintering temperatures of *F. exsecta* fall within the range −10 to −13 °C. Even in the coldest of these areas values lower than −10 °C are endured in the overwintering chambers only for 1–2 months. Similar values of these parameters were observed in the nests of *F. sanguinea*, found in a small number of habitats together with *F. exsecta*.

Similar, extremely mild overwintering conditions are typical of *F. lemani*, which inhabits dry areas of south-facing slopes, thawing in 1–2 weeks deeper than 1 m, where the overwintering chambers are positioned. The upper soil horizons of these biotopes are cooled to −18 to −22 °C, but temperatures at a depth of 1 m never fall below −10 to −12 °C.

The lowest temperatures in the nests of all the other studied species are considerably lower. In the overwintering chambers of *F. candida* and *M. bicolor* on pebbly spits of the Detrin River the lowest temperature at a depth of 40 cm, as extrapolations showed, have to be −18 to −19 °C, and values below −10 °C were observed for over 2 months. The lowest temperatures in the nests of *F. candida* in a sphagnum–dwarf-shrub larch forest on the train of a south-facing slope, in spite of the relatively deep position of overwintering chambers (30–40 cm), also reached −20 °C. The overwintering conditions of *F. gagatoides* vary within a wide range; the lowest values usually reach −16 to −18 °C in nests on sphagnum tussocks and −22 °C in dry areas of south-facing slopes. The duration

of temperatures below −10 °C in such nests is 4–4.5 months, and the duration of temperatures below −15 °C is up to 2 months.

In most nests of *M. kamtschatica* in sphagnum tussocks the temperatures were close to −16 to −18 °C, with duration of periods with temperatures below −15 and −10 °C one and two months, respectively. However, temperatures as low as −26 to −28 °C were recorded in some of the nests.

The widest ranges and the lowest values of temperatures in the overwintering chambers of ants in the Upper Kolyma are found in *L. acervorum* and *C. herculeanus*. The soil horizon they inhabit, close to the surface, is cooled to −15 to −30 °C. In the coldest areas the duration of temperatures below −20 °C sometimes reaches 2 months; below −15 °C, around 4 months; below −10 °C, up to 6 months. Still more severe are the wintering conditions of *L. muscorum*, which inhabits relict steppe areas in the Upper Indigirka.

Finally, we would like to emphasize that the temperatures in the nests even of the most undemanding species are never lower than −30 °C, which is almost half the value of the lowest air temperatures. In biotopes with the lowest temperature of the upper soil horizons lower than −30 °C ants are absent.

CHAPTER 4
ANT COLD-HARDINESS AND ITS DETERMINING PHYSIOLOGICAL AND BIOCHEMICAL FACTORS

BASIC CONCEPTS OF INSECT COLD-HARDINESS

The last Russian monograph on the cold-hardiness of insects, *Hidden Life and Anabiosis* by R. S. Ushatinskaya (1990), was published rather long ago. Because of this, and because of the rapid development of this field abroad, we decided to begin this chapter with a brief glossary of the principal notions and terms used in the world literature. They are treated in detail in a number of monographs and reviews (Lee & Denlinger, 1991; Somme, 1995; Block, 1995; Denlinger & Lee, 1998). This minimum of key term definition (Somme, 1995; Block, 1995) is needed for the subsequent presentation of results.

Cold-hardines, ability of organisms to survive low temperatures, including long exposure to them.

Freeze intolerance (freeze susceptibility), lack of ability to survive the formation of ice in bodily fluids.

Freeze avoidance, survival strategy realized by frost-sensitive species.

Freeze tolerance, ability to survive extracellular formation of ice, provoked with ice nucleating agents. The term is usually used for insects that survive freezing at temperatures lower than supercooling point.

Freezing point, temperature at which the growth of ice crystals starts in a solution.

Melting point, temperature at which a frozen solution completely melts (last ice crystals disappear).

Supercooling, preservation of liquid state in a solution at temperatures below its freezing point.

Supercooling point (crystallization temperature), temperature at which ice crystallization or spontaneous freezing starts in a supercooled system.

Supercooling capacity (depth of supercooling), difference between the supercooling point of the whole insect and the melting point of its haemolymph.

Lower lethal temperature, temperature at which an insect dies of cold.

Antifreeze, substance decreasing the freezing point of an aqueous solution.

Polyols, alcohols containing multiple hydroxyl groups (glycerol, ethylene glycol etc.) of low molecular weight, serving as antifreezes.

Cryoprotectant, substance that can protect cell structures or the whole organism from the damaging influence of negative temperatures, including freezing.

Ice nucleating agent, substances (often specific proteins) causing the ice nucleation in a supercooled system.

Thermal hysteresis, difference between the freezing point and the melting point of a solution (haemolymph or other bodily fluid).

Thermal hysteresis proteins, antifreeze proteins facilitating thermal hysteresis.

Vitrification, transformation of supercooled concentrated water solution into amorphous solid (glass) state without crystallization.

Acclimation, influence (process and effect) of gradually decreasing temperatures in a laboratory experiment, usually during several days or weeks.

Acclimatisation, the same process and effect, but at gradually decreasing seasonal temperatures in nature.

Insects of the temperate zone dwelling in climates with distinct seasonal courses of air temperature are more or less subject to the action of sub-zero temperatures in winter. Overwintering insects have two basic strategies of cold-hardiness: freeze avoidance (freeze intolerance, freeze susceptibility), or freeze tolerance (tolerating the formation—usually extracellular—of ice in the body). The reaction of insects to low temperatures is shown schematically in Fig. 35 (Lee, 1989).

Freeze-avoiding insects survive considerable cooling, remaining unfrozen in the physical sense (i.e. without ice formation). This is achieved both by decreasing the freezing point of bodily fluids through increasing their osmotic concentration and by increasing the capability of overcooling. Freezing is lethal to insects of this group. In contrast, insects capable of surviving freezing restore all their living functions after defrosting. Tolerance to the action of low temperatures is subject to seasonal variation in both groups. Typical features of the two main strategies of insect cold-tolerance are shown schematically in Fig. 36 (Block, 1995).

A common way of preparation for winter includes the accumulation of substances acting as antifreezes: polyols, sugars, amino acids in concentrations 0.5 to 4 molar (Storey & Storey, 1991). These changes reduce the chances of ice formation. In freeze-avoiding species, moreover, the number of ice nucleators decreases (Lundheim, 2002), and antifreeze proteins are sometimes synthesised (Duman et al., 1991, 2004). Antifreeze polypeptides work by forming hydrogen
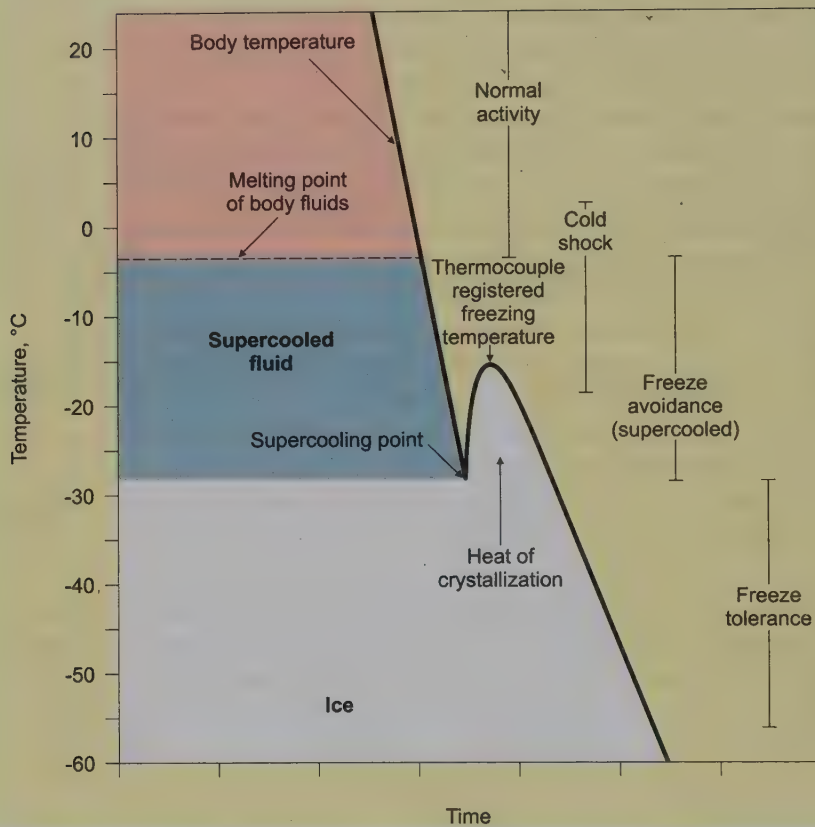
Fig. 35. Typical response of an insect to cooling below 0 °C in terms of its body temperature, activity and cold-hardiness. Possible activity ranges in different geographical zones are summarised (Lee, 1989).

bonds and by adsorptive dissolution of forming ice crystals (Davies et al., 2002). The combined action of decreased number of ice nucleators and synthesis of antifreeze proteins increases the supercooling capacity, helping these species to avoid crystallization, usually at temperatures as low as −20 to −30 °C, and sometimes even as low as −40 °C (Somme, 1982; Duman et al., 1991; Lee, 1991). The lowest values of supercooling point can reach −60 °C (Miller & Werner, 1987) and even −80 °C (Bennett et al., 2005).

In contrast, most freeze-tolerant species prepare for winter by increasing the number of ice nucleators, loss of the supercooling capacity and extracellular freezing of water at −5 to −10 °C. Polyols and sugars produced in the course of
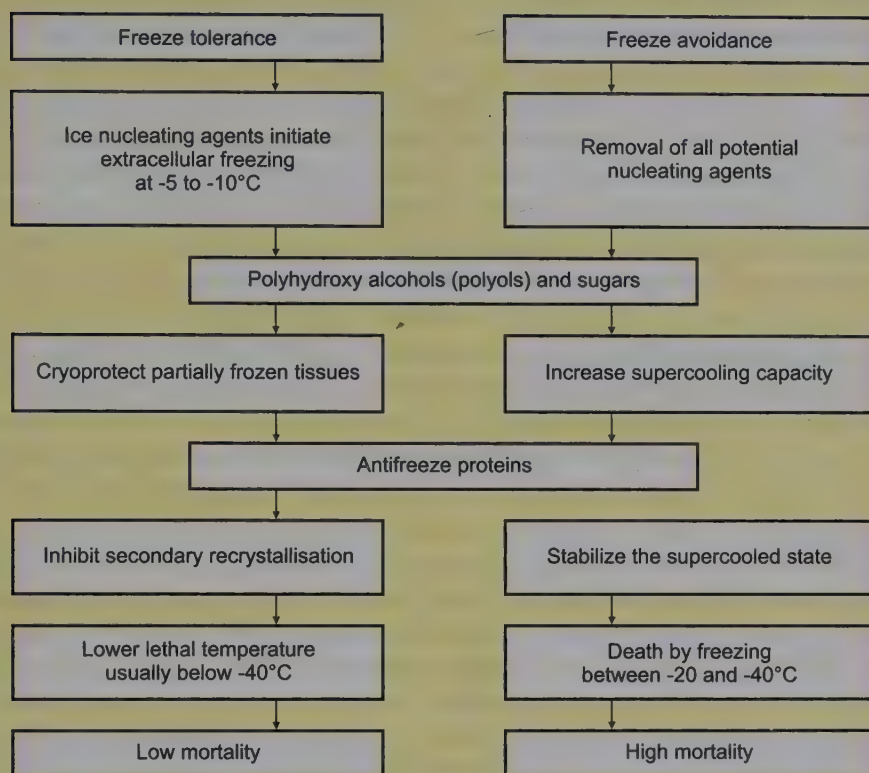
Fig. 36. Schematic representation of the peculiar features of the two basic strategies of insect cold-resistance (Block, 1995).

preparation for overwintering act as cryoprotectants, protecting partially frozen tissues. The range of the lowest tolerable temperatures is wide: from −25 to −70 °C. In species tolerating very low winter temperatures (−40 to −70 °C) antifreeze proteins are also found (Duman et al., 2004), capable of suppressing the re-crystallization of ice, the probability of which increases at temperatures around −20 °C. In addition, several species are known, mostly overwintering in the open above the surface of snow, which have both very low supercooling points (sometimes as low as −50 to −60 °C) and the ability to survive freezing (Ring, 1982; Sinclair, 1999). Both strategies have their advantages and disadvantages regarding the achieved cold-hardiness and its energy cost; some species employ both strategies (Block, 1995).

All overwintering insects undergo some degree of dehydratation. Freeze-avoiding species often display a diapause-related decrease of water content in the

course of preparation for winter; cells of freeze-tolerant species are dehydrated by partial extracellular freezing of water (see review: Danks, 2000). Differences in water balance are sometimes crucial for providing different levels of cold-hardiness in freeze-avoiding insects of different populations (Bennett et al., 2005).

Most insects of the temperate zone are subject to the influence of low temperatures during the winter diapause (Denlinger & Lee, 1998). Diapause developed in many invertebrate species precisely as a way of adaptation to seasonal changes of the environment, including seasonal low temperatures and related changes in availability of food, humidity regime etc. (Ushatinskaya, 1980). The state of diapause is a complex combination of physiological and biochemical changes, showing some degree of suppression of all the vital processes, often with complete cessation of feeding, emptying of the intestine, etc. Diapause is usually preceded by the accumulation of reserve substances, and in the course of diapause the organism switches to anaerobic metabolism. All these changes result in a non-specific increase of the tolerance of the organism to the influence of unfavourable factors of most diverse nature (from low temperatures to toxins). There are, however, many known examples both of diapause not leading to increased cold-hardiness and of considerable cold-hardiness in developmental stages and species without diapause (see Denlinger & Lee, 1998). In other words, increased cold-hardiness during diapause may be either coincidental or an integral part of the diapause program. The connection of diapause with cold-hardiness is considered coincidental if they are regulated by different environmental signals (Denlinger & Lee, 1998). However, whether diapause and cold-hardiness are coincidental or closely connected, most insects display the greatest cold-hardiness during diapause (Denlinger & Lee, 1998; Bennett et al., 2005).

In some invertebrate groups peculiar features of winter ecology and cold-hardiness have been shown to be closely connected (Kirchner, 1973; Somme, 1981; see also review: Turnock & Fields, 2005). Hardiness to the impact of low temperatures influences the spatial distribution of these animals, from geographical range to habitat distribution and choice of winter shelters (Ushatinskaya, 1980; Danks, 1978; Chen & Kang, 2005). In some species cold-hardiness both in several geographical localities with different winter temperatures and in the same locality in different seasons has been studied (see Turnock & Fields, 2005). Animals dwelling in severe conditions often have lower values of supercooling point, but it seems more surprising that populations separated by thousands of kilometres can have equal values of these parameters (Turnock & Fields, 2005).

The physiological and biochemical types of adaptive cold-hardiness strategy described above determine the methodology of studying the adaptation mechanisms of any group. Quantitative estimation of cold-hardiness requires, on the one hand, measuring the lowest temperature not lethal to the animal that

is cooled rapidly (the role of cooling rate is discussed in detail below), and, on the other hand, estimating the capacity of surviving long-term exposure to low temperatures, i.e. determine the long-term tolerable temperature. In addition, the study of the nature and content of cryoprotectants is required.

The freezing of a supercooled liquid is accompanied by the release of the latent heat of crystallization and by the decrease of temperature to freezing point (see Fig. 36), the value of which is determined by the ion concentration of the solution. The supercooling point is the lowest temperature brief exposure to which a freeze-avoiding animal can survive; freezing is inevitably lethal to such insects. Technically, the supercooling point can be easily measured with a thermocouple, which registers the jump of temperature accompanying crystallization.

The study of tolerance to long-term exposure to cold is more complicated and requires large numbers of animals. The dependence of survival rate at constantly low temperatures on the duration of exposure has been determined in some invertebrate species (Hansen & Merivee, 1971; Salt, 1958, 1966c; Hansen, 1975). Only in a few works the correlation of both parameters, tolerance to the intensity of cold and tolerance to the duration of exposure to cold, has been studied (Kuusik, 1970; Somme, 1996; Berthiaume et al., 2003). Such studies have been carried out so far only with species that can be collected in large numbers. It was found that tolerance to long-term exposure to cold changes considerably with relatively small seasonal changes of supercooling point. In periods of maximum cold-hardiness, long-term exposure to the supercooled state at temperatures 3–5 °C higher than supercooling point results in mortality. Thus, supercooling point is a representative parameter of the ecological and physiological status of freeze-avoiding species, but it cannot be used to describe freeze-tolerant species. In this group cold-tolerance is usually estimated by the temperature that kills half of the exposed individuals after 24-hour exposure, $LT_{50\%}$ (Ring, 1982).

EQUIPMENT AND METHODS OF STUDY

Supercooling point measurement. Since ants are unable to survive the formation of ice in their tissues, their cold-hardiness was estimated by the value of the supercooling point, the temperature at which the crystallization of supercooled liquid in tissues starts, measured thermoelectrically with a manganin-constantan thermocouple with precision up to 0.2 °C (Goryshin, 1966).

Thermocouple measurements of the freezing point are always in danger of underestimation. The small amount of heat released by a small freezing body, even at such cooling rate as we used, is distributed in the body (the water content of which is 30–70%) and consumed by the refrigerator. Therefore, the

registered freezing temperature can be lower than its true value. Ideally, with bodies of considerable weight and a low-power refrigerator, the cooling curve should display an isothermal section: for some time the temperature remains constant at the freezing point, until all the crystallization heat is dissipated. Precise measurement of the freezing temperature is possible either by microscopic observation of crystal growth in a liquid (extracted from an insect), or by calculation, using devices based on the principle of calorimetric bomb (e.g. differential scanning calorimeter), which register the entire flow of heat.

However, we found in the course of our work that this danger is not so high. Freezing temperatures of both the largest (*Camponotus herculeanus*) and the smallest (*Leptothorax acervorum*) ants of the northern Palaearctic, differing in mass by the factor of around 10, were very close. The cooling curve of *C. herculeanus* usually contains the isothermal section, and the freezing point of this species is apparently measured with high precision. Moreover, careful comparison showed that the freezing point of *C. herculeanus* in most nests (–32 to –35 °C) is even somewhat lower than in *L. acervorum* (–28 to –33 °C), the supercooling point of both species being –35 to –40 °C and –33.5 to –46.4 °C, respectively (Leirikh, 1989). Thus, the depth of their supercooling, i.e. the difference between the supercooling point and the freezing point, is relatively small, around 8 °C (Leirikh, 1985), whereas in members of the genus *Formica* it reaches 17.2 °C (Berman et al., 1987a). Thus, employing the same cooling conditions allows use of the obtained values as relative parameters for the comparison of series of conspecific individuals or individuals similar in size of different species.

Supercooling points were measured in ants from 165 nests, in a total of over 10 thousand specimens. The calibration of thermocouples was carried out for correcting the reference tables for copper-constantan thermocouples (Scott, 1954) with precision 0.05 °C in the range of temperatures –75 to +5 °C. The zero junction of the thermocouple was positioned in a closed vacuum flask with melting ice (triple point of distilled water 0.01 °C), the measuring junction was inserted via a hole in the stopper into a vacuum flask with 96% ethanol cooled with liquid nitrogen to –75 °C. The temperature of ethanol was controlled with a platinum TSP resistance sensor without insulating case, the parameters of which at 0 °C were previously determined with precision 0.01 Ω. To avoid the influence of temperature gradients forming in the ethanol, the measuring junction of the thermocouple was applied to the resistance sensor and fixed. Each point of the calibration curve was determined after the stabilizing the temperature in the vacuum flask by 5–7 minutes shaking. The resistance of the sensor was measured with an R-385 digital volt-farad-ohm meter with precision 0.01 Ω, and the thermoelectromotive force of the thermal couple was measured with a V7-21 digital universal voltmeter with precision 1μV.

The supercooling point was measured with an I-37 direct-current amplifier (Fig. 37) or a N3012 microampere-voltmeter and a KSPP recording two-channel potentiometer with 1 s carriage run; the output of the amplifier and the input of the potentiometer were adjusted with a voltage divider. The precision of the measurements of temperature parameters of insects, taking equipment class into account, was 0.2 °C.

The ants were cooled in a two-stage semiconductor microrefrigerator (Goryshin, 1966) or in a specially prepared freezer of a domestic refrigerator. Temperatures below −40 °C were achieved with a 20 l Dewar flask with a small (3–4 l) amount of liquid nitrogen at the bottom. This proportion of volumes creates within the flask a gradient sufficient for the experiment: the temperatures in the neck of the flask changed from 0 to −60 to −70 °C. A hollow rod of unplasticized polyvinyl chloride (outer diameter 2.5 cm) ending with a chamber containing the cooled ants was lowered step by step (first to 5–10 cm, then each time to 1–1.5 cm) into the flask with the help of a multi-purpose physical support stand. The chamber was shaped like a half of a cylinder 2 cm high; the bottom of the chamber was hermetically closed, cooling was going through a moveable front wall formed by a brass tube segment tightly fitting the rod (Fig. 38). The thermocouples were running inside the rod, their measuring junctures inserted into the chamber; above the chamber inside the rod there was a light bulb (3 V), used not only for illumination, but also for quickly warming the chamber between cooling
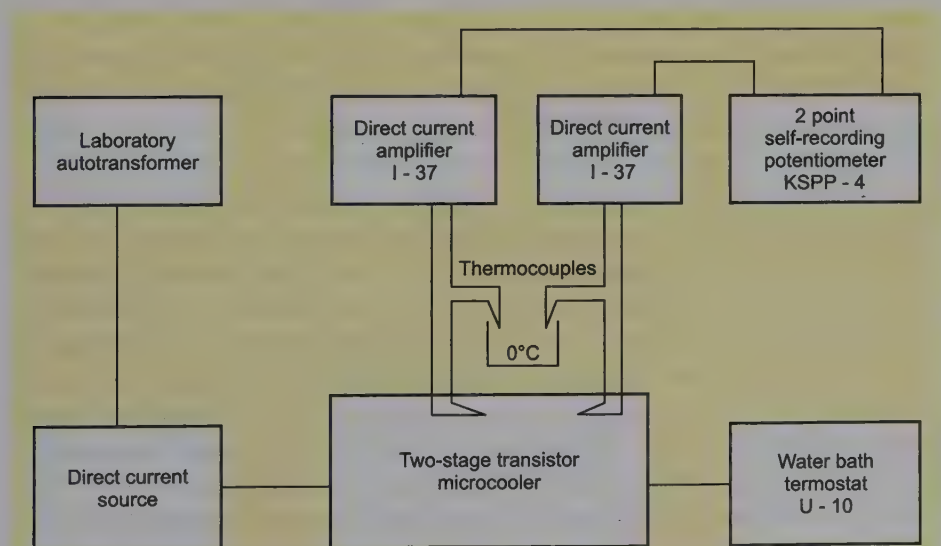
Fig. 37. Flowchart for measuring the supercooling points of invertebrates.
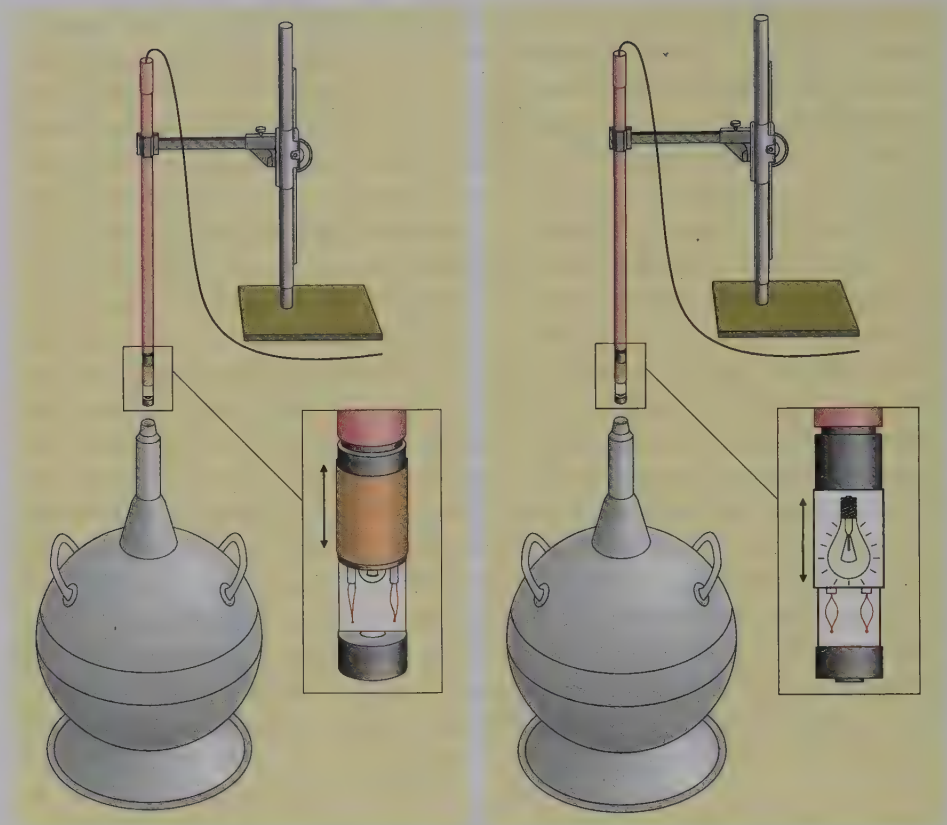
Fig. 38. Scheme of an apparatus for measuring the supercooling points, based on a Dewar flask with liquid nitrogen. The system includes cooling chambers with two thermocouples and a bulb for rapid warming.

cycles. The rate of air cooling in the chamber depended on the heat conductivity and the heat capacity of the material of the walls and on the difference of temperatures within and outside the chamber; the latter parameter was determined by the experimenter manually and allowed regulating the cooling rate within the required limits (from 0.5 to 7–10 °C per minute). Usually two animals fixed at the junctures of two thermocouples with a thin layer of petroleum jelly, which provided better heat-conducting contact, were cooled simultaneously. For more precise recording of double freezing individuals of some ant species were fixed at one thermocouple by the thorax and at the other by the abdomen.

However, measuring supercooling points with the help of thermocouples is extremely labour consuming, since every measurement implied repeating the cycle of procedures: fixing the animal, providing required cooling rates, etc. There-

fore, in those cases where the task required studying samples of many individuals, a battery of 30 series-connected thermocouples was used; all the junctures of these thermocouples were exposed to the same temperature; the temperature in the chamber was controlled by a separate "independent" thermocouple. The thermobattery was assembled by electrolysis application of a copper layer on constantan wire with removed enamel. Another possible way of assembling a thermobattery is by welding the junctures of thermocouples.

The recording part of the device consisted of two I-37 amplifiers (one for the thermobattery with a compensating block, the other for the control thermocouple) connected to two channels of a KSPP-4 recording potentiometer.

The key condition of the reliability of taking supercooling point measurements with a thermobattery as precisely as with an individual thermocouple is the exclusion of temperature gradients within the cooling chamber. We used as a cooling chamber a copper box $80 \times 80 \times 50$ mm with walls 2 mm thick, glued over with a layer of plastic (also 2 mm thick) and positioned in the freezer of a Freon refrigerator. Four individual thermocouples mounted in different parts of such a box at the distance of 1, 2 and 4 cm from the walls showed temperature differences no greater than 0.2 °C at cooling rates from 0.5 to 10 °C per minute. Such negligible temperature gradients inside the box allow it to be used for simultaneous measurements of the parameters of 15–30 animals (depending on their size and on the given cooling rate) with 30 measuring and 30 zero junctures, recording the freezing of individuals at 0.5 s intervals.

Many authors emphasize the importance of choosing the right cooling rates for measuring the supercooling points of invertebrates. The range of cooling rates is restricted by several factors. Since the probability of spontaneous ice nucleators formation in a supercooled liquid is proportional to the decrease of temperature and to the increase of exposure duration, the state of a supercooled liquid at too low cooling rates approaches its state at constant temperature, whereas too high a cooling rate creates considerable gradients within the cooled object, decreasing the precision of measurements and initiating freezing in the most cooled areas (Salt, 1966a). In accordance with this effect, R. Salt (Salt, 1966a) in his experiments with the larvae of the sawfly *Cephus cinctus* (Hymenoptera: Cephidae) had supercooling point decreasing by 0.24 °C every time the cooling rate was doubled in the range from 0.5 °C per hour to 11.5 °C per minute in series of 10–20 specimens.

Later, E. Merivee (1970) and A. Kuusik (1971) determined for bodies of different weight the allowable cooling rates, at which the gradients forming in these bodies are still too small to distort the value of the supercooling point. The cooling rates recommended by these authors are 0.2–0.5 °C per minute for 400 mg bodies, 1 °C per minute for 5–30 mg bodies, and 3–4 °C per minute for

less than 5 mg bodies. The decrease of supercooling point values with increasing cooling rate recorded by R. Salt was not observed by these authors. The above-listed restrictions of cooling rates hold true only for freeze-avoiding inverte-brates, whereas for freeze-tolerant animals, capable of surviving ice formation in their tissues, cooling rates should be no greater than 0.2 °C per minute (Miller, 1978).

Restrictions of the cooling rate are determined rather by the ratio of surface and volume, which influences the evenness of cooling, than on the weight of the body. The shape of ants (well-marked head, thorax and abdomen) is distinctly different from the shape of insects studied earlier. Therefore, we checked whether the values of cooling rates recommended for other insects are applicable to ants. This experiment was carried out with ants of markedly different average weight: *F. exsecta* (6 mg) and *L. acervorum* (0.5 mg). The supercooling points were meas-ured in the middle of winter, at the time of the lowest cold-hardiness variance (see below). The compared ants included a series of *L. acervorum* workers from the same nest and a series of *F. exsecta* not only from the same nest, but also from wintering chambers positioned in the soil at the same depth, for excluding the influence of the temperature regime of wintering. Ants were cooled at the rates of 7–8 and 0.6–0.7 °C per minute. In accordance with the results of R. Salt, average values of the supercooling point lower by approximately 1 °C could be expected in all the series of rapidly cooled animals. But in fact deviations with

Table 12. Average supercooling points of the *F. exsecta* and *L. acervorum* workers, mea-sured at different cooling rates in ants from the same nest

Species	Depth of wintering chamber position, cm	Cooling rate, °C per minute	Super-cooling point, °C m ± SE	Number of tested individu-als	Differ-ence between super-cooling points, °C	Statistical signifi-cance level, %
F. exsecta	5	7	−18.6±0.6	33	2.1	97.1
	5	0.7	−20.7±0.4	58		
	10	7	−20.5±0.5	60	0.4	44.5
	10	0.7	−20.9±0.4	63		
L. acervorum	10	7	−38.1±0.4	37	1.2	89
	10	0.7	−39.3±0.6	32		
	7	7	−38.7±0.4	38	1.9	99
	7	0.7	−36.8±0.6	32		

different significance levels (Table. 12) were observed, including both higher (by 1.9 °C in *L. acervorum*) and lower (at most by 2.1 °C in *F. exsecta*) values of the supercooling point. These differences were, evidently, statistical, i.e., resulting rather from the considerable dispersal of cold-hardiness of the studied individuals (see below), than from different cooling rates, the effect of which within this range of cooling rates was too small to be distinguishable in the experiment.

Thus, cooling rates from 0.7 to 7 °C per minute can be used in experiments with ants of body weight up to 5–6 mg. The actual cooling rates used in our study were 1–3 °C per minute.

Determination of ant mortality under low sub-zero temperatures. Although supercooling point is the most commonly used measure of the cold-hardiness of invertebrates overwintering in an unfrozen state, this parameter is not sufficient in those cases where the difference between the supercooling point and the actual temperature of overwintering is small. Supercooling point indicates only the capacity of surviving short-term exposure to low temperatures, which is the case in organisms overwintering in rapidly changing conditions, e.g. in the open air. Organisms protected by layers of snow and soil are insured against abrupt changes of temperatures, but lowest values can persist in the soil for long periods of time (up to several days). Therefore, estimating the actual ecological situation of these organisms requires determination of the correlation between supercooling points and long-term tolerance to low temperatures.

For this reason, we determined in most ant species not only supercooling point, but also mortality from exposure for over 24 hours to temperatures close to the average supercooling point. Both parameters were determined simultaneously in animals from the same nest.

The facility for determining the mortality of invertebrates includes a set of low-temperature chambers (Fig. 39), where animals can be kept indefinitely long at a series of temperatures differing by 3–5 °C. We used domestic compression refrigerators with additionally heat-insulated evaporators and replaced automated mechanisms as temperature-coltrolled chambers. These relatively simple additions to their design allowed maintenance of a particular temperature in the freezer with precision 2 °C. However, because of the fluctuation-smoothing effect of the copper boxes containing the animals, the temperatures to which they were exposed could vary only by 0.2 °C. For determining the relationship between exposure duration and the number of frozen ants a battery of series-connected thermocouples was inserted in each of the above-described boxes. In addition, series of insects were exposed to the same temperatures without recording the freezing of individuals, estimating only the integral result, i.e. the distribution of the number of peaks depending on the
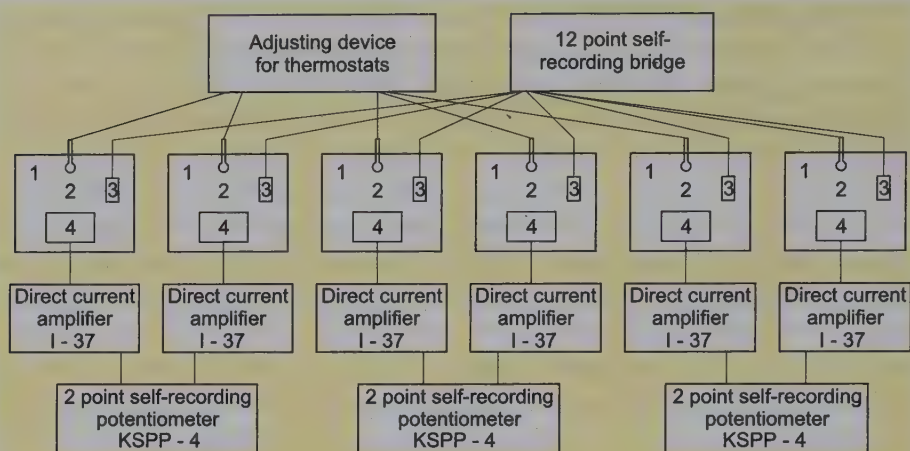
Fig. 39. Flowchart of an apparatus for measuring the survival rate of invertebrates under different temperatures and exposure durations. Key: 1, low-temperature thermostat based on a domestic refrigerator; 2, contact thermometer; 3, control resistance temperature detector (TSM); 4, battery of thermocouples.

value of temperature. After exposure to low temperatures, all the insects were revived in standard laboratory conditions.

Analysis of the chemical composition of ants. It is well known that the cold-hardiness of many invertebrate species depends on several physiological and biochemical factors. It is mainly facilitated by such factors, connected with the state of diapause, as decrease of water content and accumulation of polyols (in particular, glycerol and sorbitol), monosaccharides and amino acids, as well as, to some extent, certain changes in the content of fatty substances. The percentage of water was measured according to the standard procedure: by weighing live animals and animals dried at 100 °C. The total content of polyols was determined spectrophotometically by the colour reaction of formaldehyde produced by periodate oxidation of polyols with acetylacetone (Vaskovsky & Isay, 1969); the content of glucose was determined also spectrophotometrically by the o-toluidine method (Pryce, 1967). Glycogen was extracted with 30% solution of potassium hydroxide and quantitatively estimated by the amount of glucose produced by acid hydrolysis with 2 N sulphuric acid (Mosin & Petrova, 1980). Lipids were extracted with a hexane/acetone mixture (Hara & Radin, 1978), and their total quantity was estimated nephelometrically (Canal et al., 1972).

The qualitative composition of polyols was determined by micro-thin-layer chromatography with standard substances of known retardation factor on silica gel plates (Kates, 1975) impregnated with sodium phosphate in a system of

isopropyl, acetone and water in proportion 6 : 3 : 1 (Lato et al., 1969); polyols were stained with aniline phthalate (Khromatografiya..., 1965).

Antifreeze proteins sometimes also take part in the stabilization of the supercooled state, but we did not determine their presence.

DEPENDENCE OF TEMPERATURE PARAMETERS OF ANT COLD-HARDINESS ON THE COMPOSITION OF THE STUDIED SAMPLES

It is known that the temperature parameters of invertebrate cold-hardiness often depend to a large extent both on the physiological state of animals and on characteristics of study methods, such as the rate of cooling (Ushatinskaya, 1980; Salt, 1966b). The causes of the physiological heterogeneity of populations are quite diverse. The cold-hardiness of many invertebrate species is related to the presence of reserve cryoprotectants. The quantity of these substances accumulated by an individual, as was shown by T. Hansen and M. Viik (1981a, 1981b) in *F. aquilonia*, is influenced by the timing of the start of wintering. The cold-hardiness of a number of ant species depends on how full the crop is (Maavara, 1971). It is easy to hypothesise the existence of many other causes of individual differences in ant cold-hardiness. As we found in the course of this study, the heterogeneity of physiological state in ants of different species can be observed within families, nests from the same area, and, especially, nests from areas with different temperature conditions. Some of the most revealing results, which should be taken into account in analysing ant cold-hardiness, are given below.

Effect of fullness of the crop on the cold-hardiness of ants in summer. Considerable variations of non-specific cold-hardiness reflecting different degrees of fullness of the crop were observed in ants in active state. V. Maavara (1971) showed that in a number of ant species, including *F. aquilonia*, individuals with full and empty crops were distinctly different in supercooling point, −8.6±0.4 °C in the former and −15.8±0.4 °C in the latter (measurements taken in early October). In contrast to these results, we found in samples collected from nature no division into groups with different values of supercooling point reflecting the degree of fullness of the crop in any of the ant species found in the upper reaches of the Kolyma, even in members of the genus *Formica*, which display extremely wide ranges of supercooling point variation.

Two peaks of heat release are observed in the course of cooling in some insects. The essence of two-stage freezing was first described in *Camponotus obscuripes* (Ohyama & Asahina, 1972). This effect is determined by the morphology of the ant crop, which prevents the penetration of ice nucleators from the

food, which freezes first, further down the digestive tract. These authors identified the two peaks by differential temperature analysis and microscopic study of sections. A small depth of supercooling and small, compared to the freezing of body tissues, amount of released heat are characteristic of the peak reflecting the freezing of crop contents in ants.

We carried out a number of experiments with active ants to reveal the role of food in their cold-hardiness. Samples of workers of each species were divided into two groups. The temperature parameters of cold-hardiness were measured immediately after the ants were collected in the first group and after 1–3 hours of free feeding with sucrose solution in the second group.

Only in one of the four studied ant species, *F. exsecta*, large amounts of food in the crop sometimes resulted in changes of cold-hardiness parameters. A series of *F. exsecta* workers taken from nature had an average supercooling point −12.9±0.8 °C (n = 33), most of the individuals (31) were considerably overcooled; the average supercooling point was −13.7 °C, and the freezing point was −4.6 °C, i.e. the depth of supercooling was − 9.1 °C (Fig. 40). A small proportion of the ants were frozen at higher temperatures (−2 to −4 °C), with a depth of supercooling only 1–1.5 °C. The peak of heat release with small depths of supercooling, reflecting the freezing of the crop content, was observed at −10.8 °C in one third of the individuals.

The second group of ants (which had been feeding) had virtually the same supercooling point (−13.1±0.5 °C, n = 40), but the proportion of individuals freezing at high temperatures with small depths of supercooling was increased to 30%, whereas the average supercooling point in the remaining 70% decreased by 3 °C, compared to the first group (significance level 89%). The peak reflecting the freezing of the crop content was observed in 88% of all the feeding individuals; its supercooling point decreased to −14.5 °C. Thus, in most ants of the second group the freezing of food in the crop took place already after the freezing of tissues, i.e. in reverse order, compared to ants of the first group.

Adults of two other members of the genus *Formica*, *F. candida* and *F. gagatoides*, taken in summer from nature, displayed still lower supercooling points (−16 to −18 °C) than *F. exsecta*, with supercooling capacity 10–11 °C (see Fig. 40). In ants of these species feeding did not increase the proportion of individuals freezing at high temperatures, but only decreased supercooling point and depth of supercooling by 2–3 °C. The increase of the depth of supercooling was especially noticeable in *F. gagatoides*. The sample of this species taken from nature was divided into two groups based on this character: in 40% the depth of supercooling was only 7 °, whereas in the remaining 60% it was 14 °C. The depth of supercooling of feeding individuals was 13.7 °C.

The peak reflecting the freezing of the crop content was observed in 40% of ants from nature and in 90% of ants that had been feeding. In both species this peak always preceded the freezing of body tissues, the peak of feeding

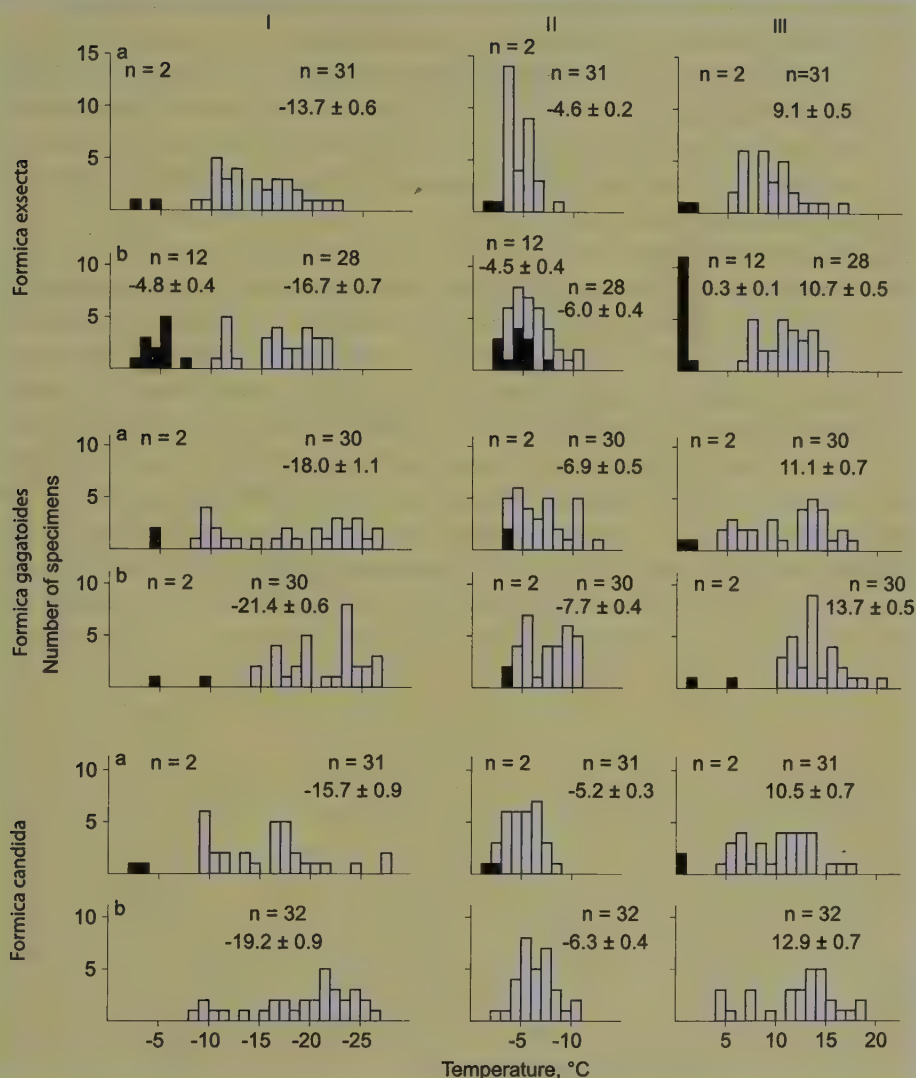**Fig. 40.** Distribution of supercooling points (I), freezing points (II) and depth of supercooling (III) in workers of *F. exsecta, F. gagatoides* and *F. picea*, taken from natural conditions (a) and fed with sucrose solution (b). Parameters of specimens with small depth of supercooling are shaded. Figures show the size of samples in each group and average supercooling points with mean error values.

individuals differing in its somewhat greater depth and in slight decrease of temperature.

Myrmica kamtschatica displays summer cold-hardiness different from that described above for ants of the genus *Formica*: average supercooling point of workers (Fig. 41) was only −8 °C, and their depth of supercooling at most 4.5 °C. The release of heat reflecting the freezing of the crop content was observed in 40% of individuals, at the average temperature of −9.4 °C and, thus, often followed the freezing of tissues. In ants fed with sucrose solution the supercooling point both of tissues and of the crop content was slightly (on the average by 1 °C) decreased; the peak reflecting the crystallization of the crop content was observed in 80% of individuals.

Thus, in all the studied ants the freezing of the crop content takes place independently of the freezing of tissues and sometimes later. In ants (unlike many other insects) the presence of food in the crop does not result in an elevated supercooling point due to the spreading of crystallization starting in the crop to body tissues. Only in workers of *F. exsecta* food contained in the crop raises the supercooling point in some individuals and decreases the difference between the supercooling point and the freezing point. Feeding with sucrose solution results in some decrease of the supercooling point; it is natural to suppose that this happens because of increased concentration of sugars in the haemolymph.

The revealed dependence of average supercooling point on the proportion in the sample of individuals with full and empty crop partly explains considerable
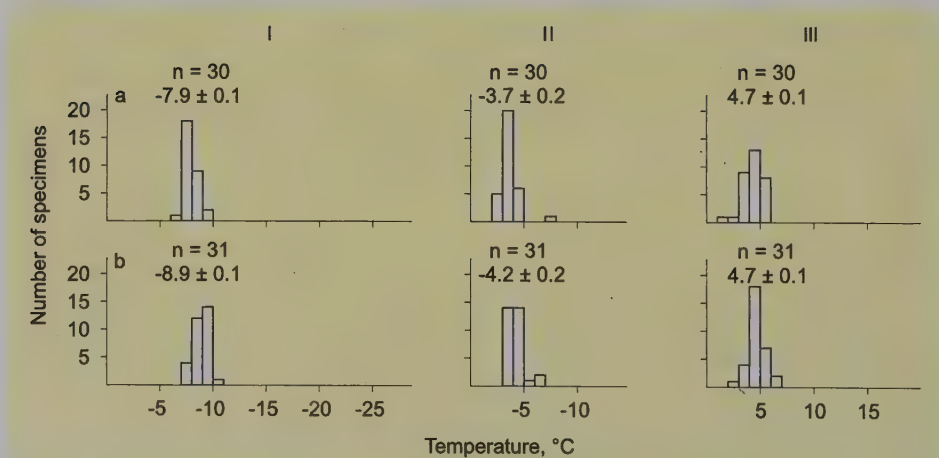

Fig. 41. Distribution of supercooling points (I), freezing points (II) and depth of supercooling (III) in *M. kamtschatica* workers taken from natural conditions (a) and fed with sucrose solution (b). Other notation as in Fig. 40.

variations in the summer cold-hardiness observed in ants, especially in members of the genus *Formica*.

Differences in the cold-hardiness of ants from different parts of the nest. It has been shown that the layer where ants overwinter can be at different depths, from 5 cm to 1.5 m, depending on the species and the locality where the nest is built. The thickness of this layer in large nests is 15–20 cm, and lowest temperatures within it may differ by 1–3 °C, which may result in differences in the cold-hardiness of overwintering ants.

We studied this in the nests of *F. exsecta* and *C. herculeanus*. No distinct tendency for change of the supercooling capacity with increasing depth of overwintering chamber position (i.e. with increase of the lowest soil temperatures) was revealed. For instance, in a nest of *F. exsecta*, where the lowest temperatures in overwintering chambers differed by 1.1 °C (Table 13), the lowest average supercooling point was found in ants from the deepest chamber, whereas the highest supercooling point was found in ants from chamber 3 in the middle of the nest. The average supercooling points of ants from chambers 1 and 5, positioned higher and lower than chamber 3, were equal and lower than the average of the whole nest.

A still more heterogeneous pattern was found in a nest of *C. herculeanus*, which had 10 overwintering chambers positioned at the base of a larch stump at a depth of 5–10 cm. The temperature conditions of overwintering differed little, and the lowest recorded temperatures were −16 to −18 °C. Cold-hardiness was measured in ants from four chambers containing the greatest number of individuals. The freezing of adult *C. herculeanus* in winter usually goes in two stages: first, at −10 to −12 °C the crop content freezes, with depth of supercooling 1.5–2 °C, and then, at lower temperatures, body tissues freeze, with greater depth of supercooling. In the studied nest, 132 (71.4%) of the 185 wintering individuals froze in two stages, with supercooling point −33.9±0.4 °C; 13 individuals (7%) froze also in two stages, but with peak depth smaller than 2 °C and with supercooling point −27.5 °C; in 28 individuals (15%) tissues froze simultaneously with crop content (average supercooling point −18.6 °C); 12 individuals (6.5%) were probably dead: they displayed no temperature jump. The distribution of the ants of these groups in overwintering chambers was extremely irregular (Fig. 42): individuals in the best condition were from chambers 6 and 8, whereas chamber 4 contained the greatest number of dead individuals and those freezing in one stage. It should be noted that in spite of such a diverse composition of ants in the overwintering chambers, the average supercooling point of the individuals freezing normally, in two stages, varied little (−37.8 to −39.3 °C). This result leads to an important conclusion: a sample of 30–50 individuals is
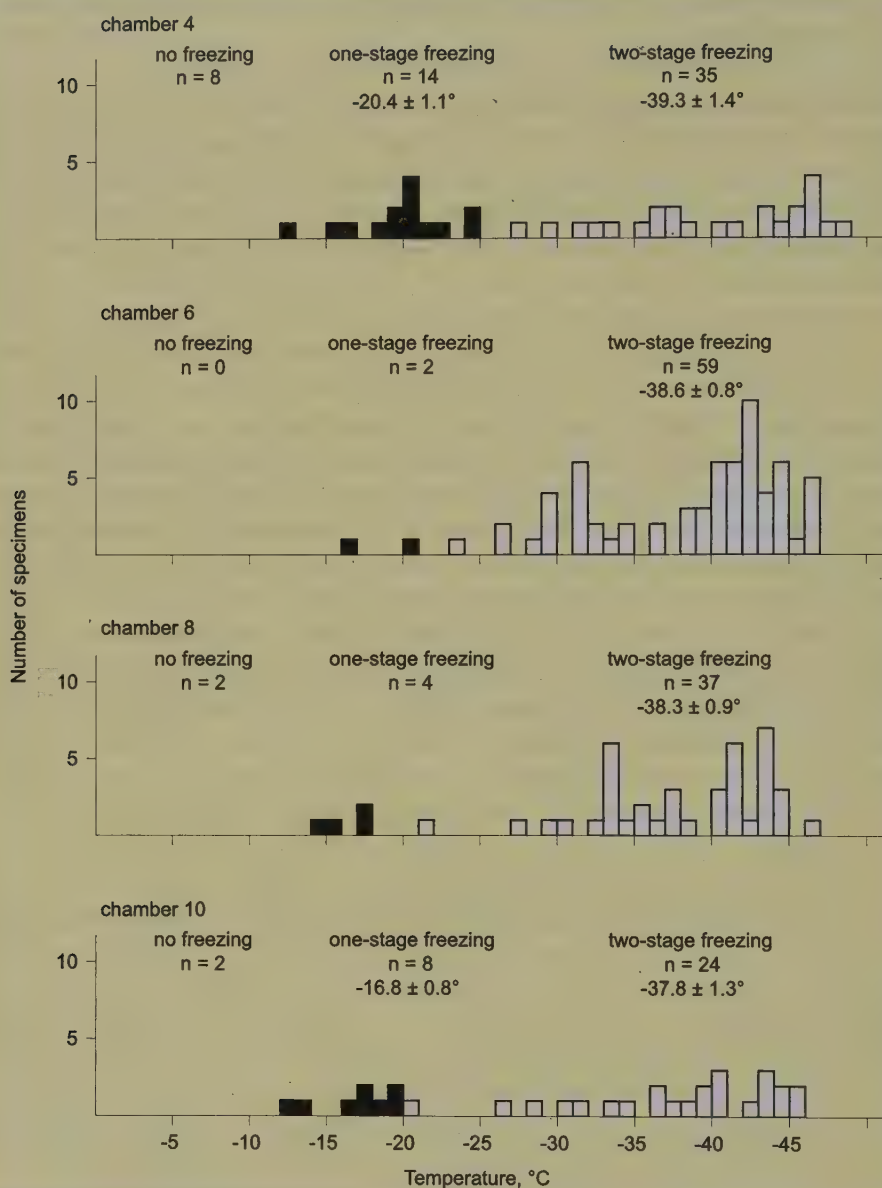
Fig. 42. Distribution of the supercooling points of *C. herculeanus* workers from four chambers of the same nest (February 1981). Supercooling points of individuals with one-stage freezing shown in black; other notation as in Fig. 40.

Table 13. Average supercooling points of *F. exsecta* workers from the same nest, overwintering in chambers positioned at different depth

Chamber no.	Depth of chamber position, cm	Supercooling point, °C m ± SE	Number of tested individuals	Lowest winter temperature in chamber, °C
1	0	−20.9±0.4	59	−9.9
2	5	−20.7±0.4	58	−9.0
3	5	−18.6±0.4	33	−9.0
4	10	−20.5±0.5	60	−8.9
5	10	−20.9±0.4	63	−8.9
6	13	−21.4±0.4	62	−8.8
1–6	0–13	−20.7±0.2	335	

representative of the cold-hardiness of the viable part of the nest, but not of the winter mortality in the whole nest.

Differences in the cold-hardiness of ants from different nests in the same area. The greatest variation in winter cold-hardiness within a single area with relatively homogeneous temperature conditions was found in *L. muscorum*, overwintering in the soil at a depth of 7–10 cm under the cover of snow around 30 cm thick at lowest temperatures reaching −25 °C. The average supercooling points in ants of this species from six studied nests were −36.7±1.0 (n = 27), −37.9±1.6 (n = 20), −39.3±0.6 (n = 29), −41.2±0.7 (n = 23), −41.4±0.7 (n = 24) and −42.1±0.9 °C (n = 24) (Berman et al., 1982).

The overwintering conditions and cold-hardiness of *F. exsecta* were studied in a dwarf-shrub–sphagnum larch forest in the depression of Jack London Lake, 850 m above sea level. In ants from three nests of this species, with lowest temperatures in the overwintering chambers reaching −8 to −10 °C, the average supercooling points were −19.4±0.4 (n = 179), −19.4±0.4 (n = 141) and −20.7±0.2 °C (n = 335). The differences between these values are smaller than the differences between chambers of the same nest (see Table 13).

Evidently, the greatest variation of the average supercooling point is found in ants from nests with few individuals overwintering close to the surface of the soil, while the variation of this parameter in ants from large nests with overwintering chambers positioned in a relatively thick layer of soil is smaller.

Close values of cold-hardiness parameters in ants from nests of the same area are observed only in winter, while in transitional periods (spring and autumn) even ants from nests positioned close to each other display considerable differences in cold-hardiness. For instance, on September 6–9, with average daily air

temperature 2–5 °C, in individuals from four nests of *L. acervorum* in a dwarf-shrub–sphagnum larch forest, the average supercooling points were −15.3±1.0 (n = 25), −17.9±0.8 (n = 37), −24.1±0.8 (n = 26) and −26.8±0.8 °C (n = 29).

Dependence of the cold-hardiness of overwintering ants on microclimatic conditions. In the upper reaches of the Kolyma the lowest soil temperatures at the depth of 10 cm are −9 to −10 °C in wet areas with thick snow cover and −33 to −36 °C in rubbly areas without snow cover. The supercooling points of workers and larvae of *L. acervorum* from nests positioned in areas differing in the lowest values of soil temperatures were measured in late February of 1981. One group of nests was in a dwarf-shrub–sphagnum larch forest in the depression of Jack London Lake and the other was in a dwarf-shrub–sphagnum larch forest on the train of a south-facing slope in the valley of the Olen River, 500 m above sea level. The lowest soil temperatures at a depth of 5–7 cm, where ants of this species overwinter, reached −12 to −14 °C in the first area and as low as −20 to −25 °C in the second area, due to the lower altitude and, consequently, lower air temperatures and smaller thickness of the snow cover.

The average supercooling point was −39.2±0.2 °C in 192 workers from six nests of the first area and as low as −41.2±0.2 °C in 190 workers from six nests from the second area, the difference significant at a level greater than 99.99%. The greatest difference between the average supercooling point of adults from nests of the same area was 2.2–2.7 °C (Fig. 43), and the values recorded for the two areas do not overlap: the lowest average supercooling point in nests of the warmer area, −40.5 °C, equalled the highest in nests of the colder area. The cold-hardiness parameters of larvae varied even more than those of adults; in the second (colder) area they were close to the parameters of adults (average supercooling point −41.3±0.4 °C, n = 198), while in the first area they were considerably higher than those of adults (average supercooling point −35.1±0.4 °C (n = 357).

Thus, the considerable variation in supercooling points observed in summer reflect differences in the state of individuals. Feeding with sucrose solution increases cold-hardiness in most species. In winter differences between average supercooling points of ants from different chambers of large nests reach 3 °C, but the value of this parameter does not correlate with the temperature conditions of the chamber. The average supercooling points of ants of the same species from different nests within a single area with homogeneous wintering conditions can differ by 5 °C (*L. muscorum*) or less; it is more variable in species with few individuals in nests and with overwintering chambers close to the surface. Differences in cold-hardiness displayed by ants of the same species inhabiting areas of the same region with different overwintering conditions are
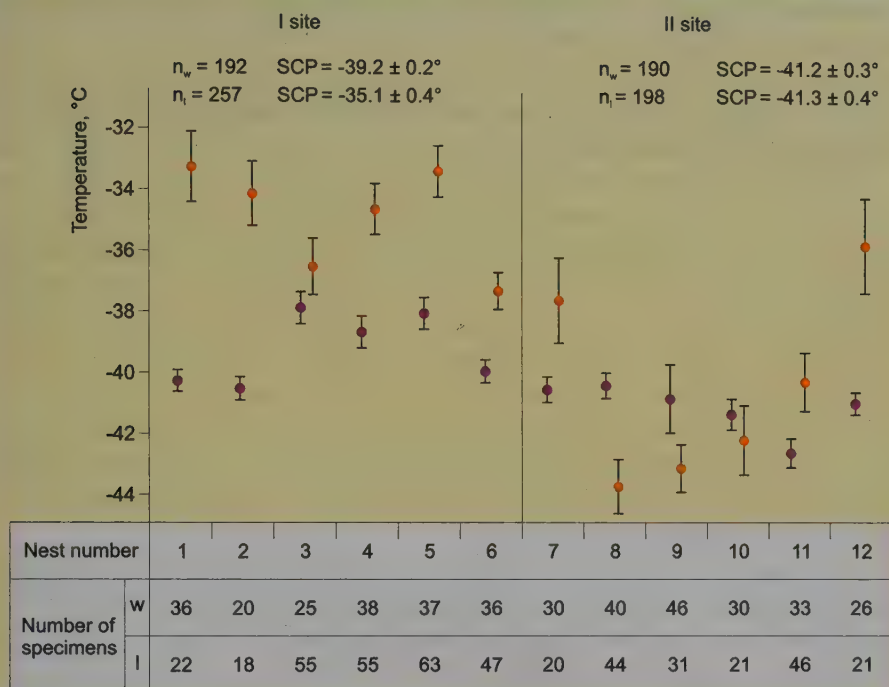
Fig. 43. Average supercooling points (SCP) of *L. acervorum* workers and larvae from nests with different winter temperatures (for explanations, see text). Lilac circles and subscript "w", workers; orange circles and subscript "l", larvae. Vertical lines hereinafter indicate standard error.

also great. Therefore, studies of the cold-hardiness of invertebrate populations from remote geographical areas have to start by revealing the variation of their cold-hardiness in contrasting habitats of each region.

SEASONAL CHANGES AND DETERMINING PHYSIOLOGICAL AND BIOCHEMICAL FACTORS OF THE COLD-HARDINESS OF ANTS IN THE UPPER KOLYMA REGION

As we mentioned above, the cold-hardiness of ants undergoes considerable seasonal changes. All the studied species of ants are divided into two groups on the basis of their summer and winter values of supercooling point, linear or step curve and range of the seasonal changes of this parameter, and the way of providing winter cold-hardiness. One group includes *L. acervorum*, *L. muscorum*, *C.*

herculeanus and both species of the genus *Myrmica*, and the other group includes all the species of the genus *Formica*.

Seasonal changes in the cold-hardiness of ants from the genera *Myrmica*, *Camponotus* and *Leptothorax*.

Summer. The state of overwintered ants in late May and early June, soon after the end of their overwintering, is clearly most "synchronised": they all start their intense vital activities. From this period to mid-July the highest average supercooling points are observed: around −5 °C in workers of *L. acervorum* and *M. kamtschatica* and −7 to −8 °C in workers of *C. herculeanus* and *M. bicolor*, freezing temperatures of all the species fall within the range −3 to −5 °C. The summer cold-hardiness of workers varies little within nests of *L. acervorum* and both *Myrmica* species and somewhat more within nests of *C. herculeanus*. However, average supercooling points differ considerably between nests even during the first half of summer, from −5.0 to −13.0 °C, and this range is identical in all the species of this group (Figs. 44–47).

In the first half of the summer the brood of this group of species includes only overwintered larvae of the same (third) instar, but of distinctly different sizes. Their average supercooling points usually fall within the range −8.5 to −12 °C, sometimes with considerable deviation; for instance this parameter was as high as −5.5 °C in a nest of *L. acervorum* examined in late July, and as low as −19 °C in a nest of *M. kamtschatica* examined in mid-July. The wide range of average supercooling points observed in summer reflects the considerable heterogeneity of the physiological state of ants, including larvae, which is probably related to the complex organization of ant families. For instance, studies using vital dyes show that a nest can contain non-feeding larvae at any period of time, while different groups of the larvae are at any period of time actively fed and warmed by the workers. Weather conditions also play some part in determining the physiological state of ants.

The bodies of ants in summer, when they are active and have little cold-hardiness, contain the greatest proportion of water, around 70% in *C. herculeanus* and 58–60% in *L. acervorum* and *M. kamtschatica*. The content of polyols, related in many invertebrate species to their tolerance to the action of low temperatures and subject to seasonal changes correlated with changes in cold-tolerance, reaches in summer at most 0.3–0.5% both in adults and in third instar larvae. The amount of glycogen, used, along with lipids, as a reserve substance, and largely determined both by external factors and by age and other individual features (Hansen & Viik, 1981b), differs within samples by 1–3%.

Autumn. The variability of temperature parameters of cold-hardiness observed in summer makes it impossible to determine with certainty the moment

when preparations for overwintering start. However, diapausing larvae of *L. acervorum* and *M. kamtschatica*, easily identified by their habitus, are found in great numbers already in early August. The occurrence of such larvae indicates that diapausing workers are also present in the same nest (Kipyatkov, 1981). Early August is also the time when supercooling points and freezing points

Fig. 44. Seasonal changes of cold-hardiness (A) and carbohydrates and water content (B) in workers and larvae of *M. kamtschatica*. Blue circles and SCP, supercooling points, orange circles and FP, freezing points.

tend to decrease in all the species, reflecting changes in the chemistry of the organism and accumulation of different reserve substances (fats, glycogen and carbohydrates).

The greatest and most rapid changes in cold-hardiness in ants of this group are observed during the first half of September, when average daily air tempera-

Fig. 45. Seasonal changes of cold-hardiness (A) and carbohydrates and water content (B) in workers and larvae of *M. bicolor*. Other notation as in Fig. 44.

ture decreases to 5–7 °C. In this period the average supercooling points of *L. acervorum* shift into the range –15 to –27 °C in workers and –12 to –26 °C in larvae. Unfortunately, we examined in this period only one nest of *C. herculeanus*

Fig. 46. Seasonal changes of cold-hardiness (A) and carbohydrates and water content (B) in workers and larvae of *C. herculeanus*. Other notation as in Fig. 44.

and only one nest of *M. kamtschatica*, which is not sufficient for conclusions about the range of changes characteristic of these species. Our results provide evidence only of the increase of cold-hardiness: the average supercooling point was −17.6 °C in workers and −15 to −30 °C in larvae of *C. herculeanus* and −21.6 in workers and −19.5 to −22.4 °C in larvae of *M. kamtschatica*.
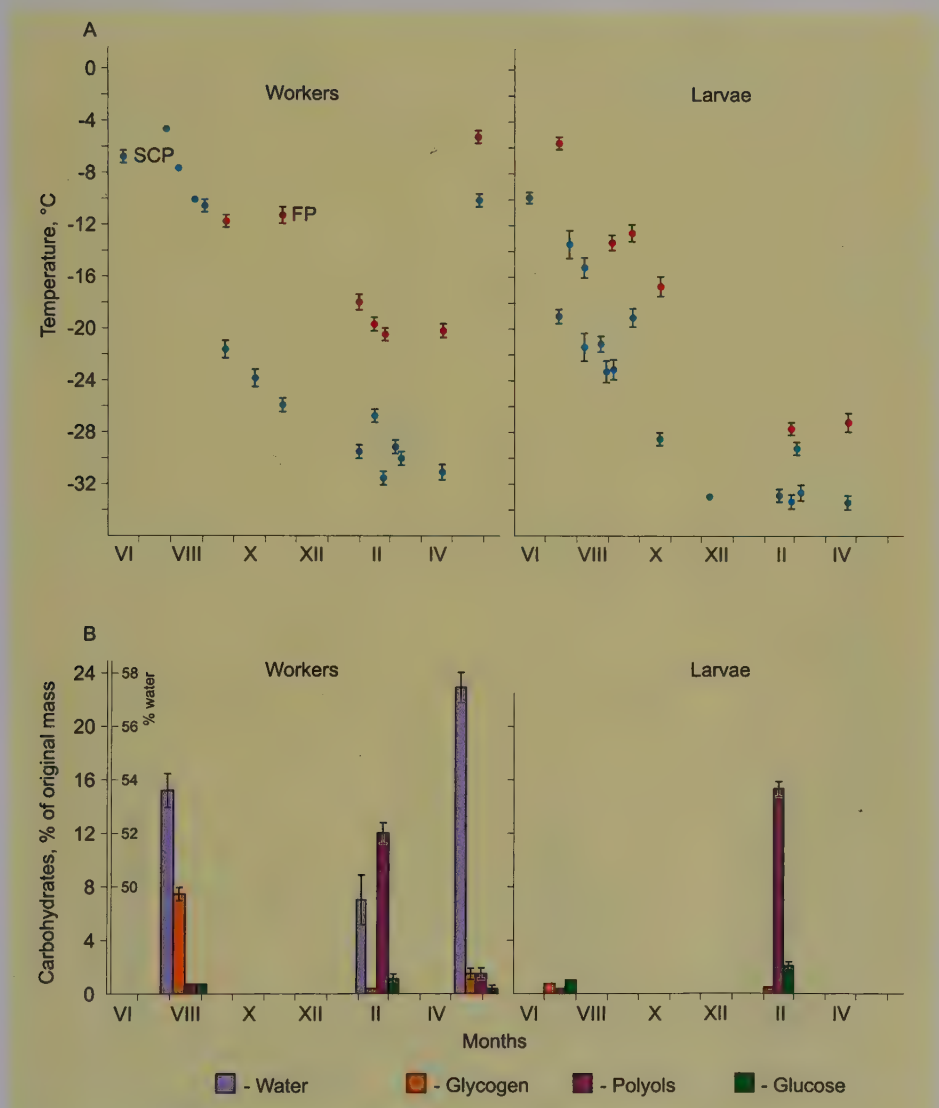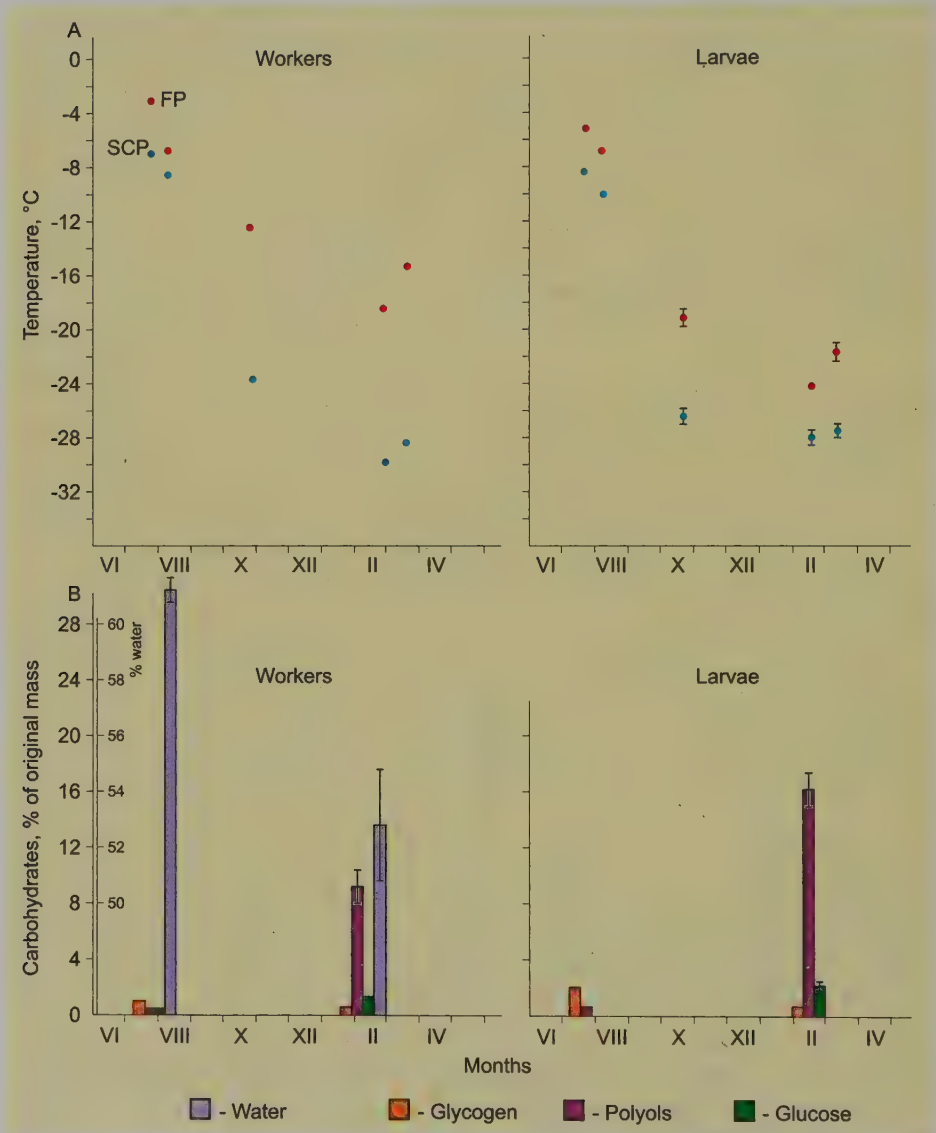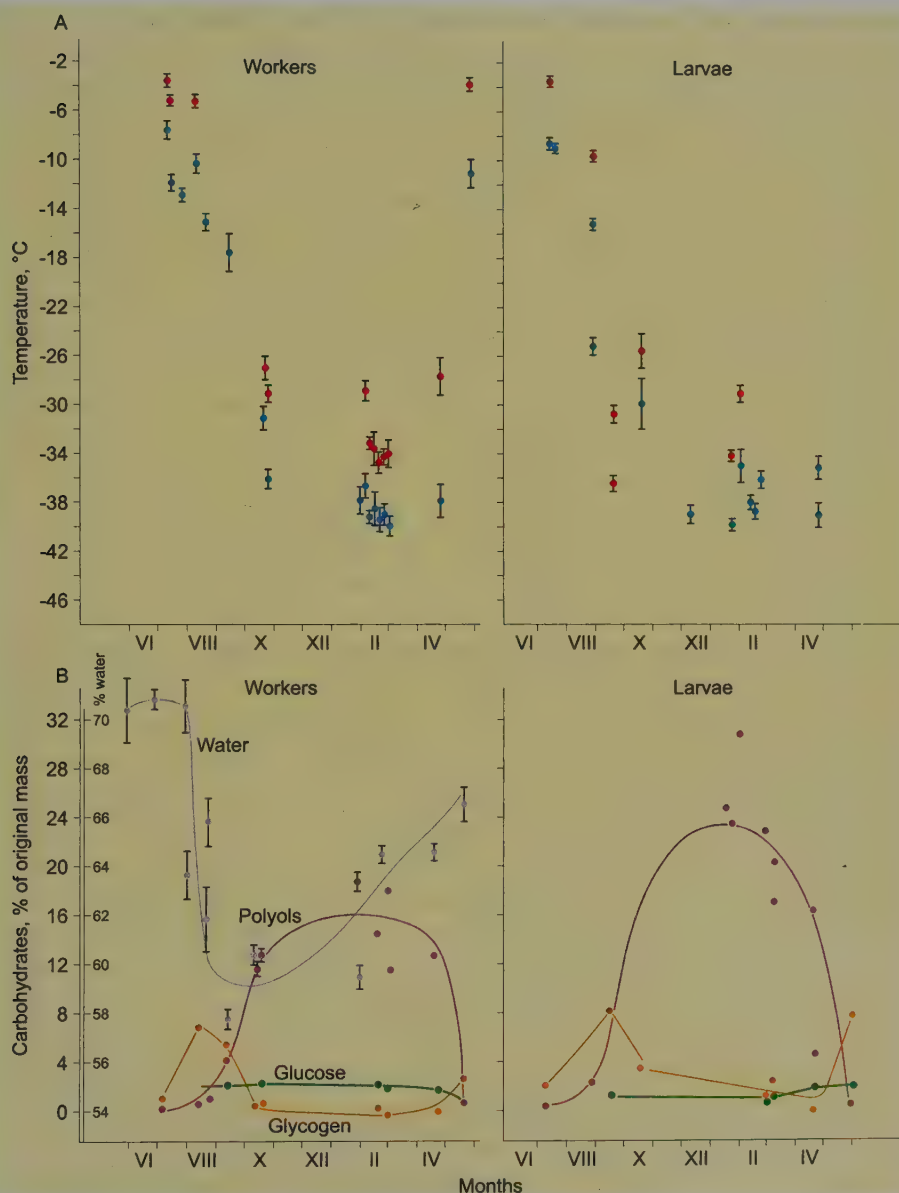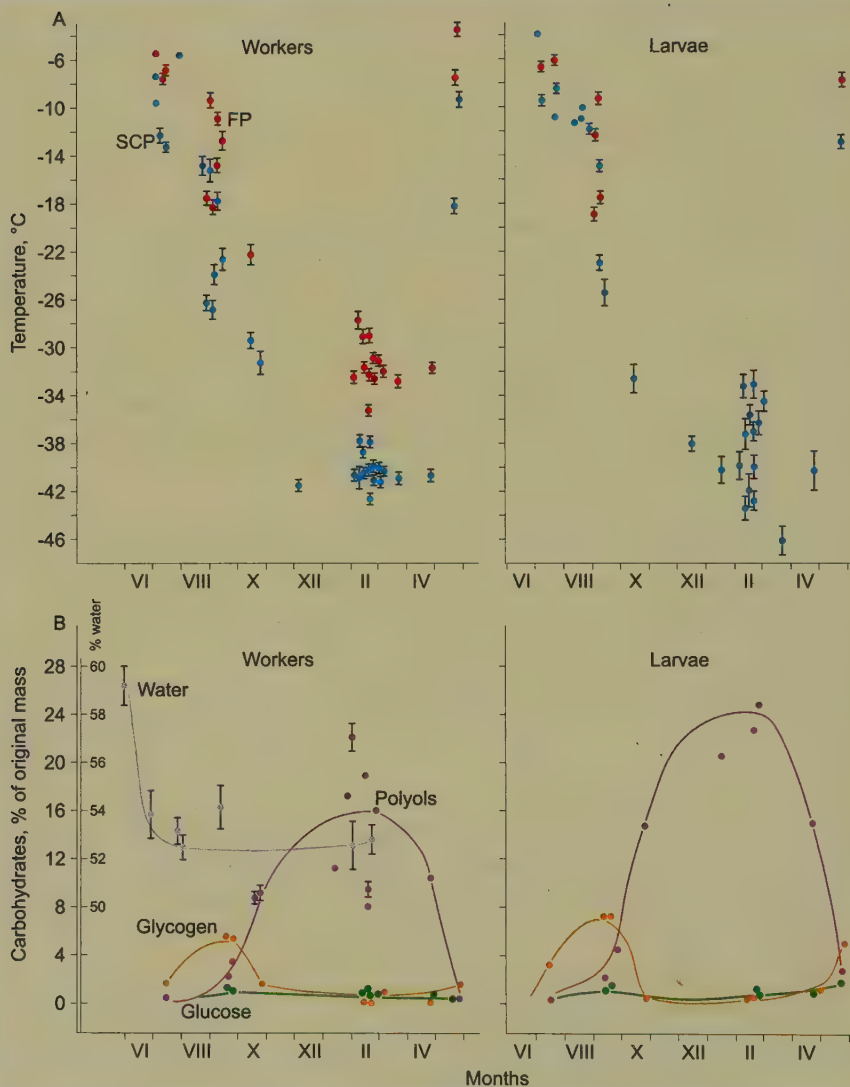

Fig. 47. Seasonal changes of cold–hardiness (A) and carbohydrates and water content (B) in workers and larvae of *L. acervorum*. Other notation as in Fig. 44.

Changes of cold-hardiness result from the complex combined action of a number of physiological and biochemical changes, reflected in the content of water and reserve and cryoprotectants. In autumn the increasing cold-hardiness of this group is related to the decreasing water content (at most by 13% in adults of *C. herculeanus* and by 7–8% in *L. acervorum* and ants of the genus *Myrmica*), the accumulation of large amounts of glycogen, somewhat greater in larvae (7–8% compared to 6% in adults), and the start of polyol synthesis (up to 3–4% in adults of *L. acervorum* and *C. herculeanus* and larvae of *L. acervorum*, and 10% in larvae of *C. herculeanus*). The content of glucose in workers and larvae of all these species is around 1–2% during this period.

The changes in the cold-hardiness of *L. acervorum*, *C. herculeanus* and *M. kamtschatica* observed in autumn are probably related to the deep diapause these species undergo. It is known that in many overwintering insects the state of diapause is induced in autumn by certain external and internal factors but when the temperature of the environment falls to 0 °C diapause is replaced by oligopause, a state of dormancy less profound than diapause, but connected with the synthesis of specific cryoprotectants (Ushatinskaya, 1973, 1980). In accordance with this two-stage change of the organism's state, cold-hardiness also changes in two stages.

In nests of different ant species the temperature usually falls below zero from early to late October, depending on the depth of the position of overwintering chambers, and in the deepest nests of *F. exsecta* this moment can be delayed until late November. By then the average supercooling point of *L. acervorum* workers reaches –29.5 to –31.5 °C, with freezing point reaching –22 °C; both parameters change by 15–18 °C, compared to their summer values. The supercooling point of larvae decreases to –33 °C (by over 20 °C). The cold-hardiness of *C. herculeanus* workers in the second half of October is even greater than in *L. acervorum*: supercooling point –31 to –36 °C, freezing point around –28 °C, difference from summer values 21–23 °C. The supercooling point of the larvae of this species reaches at this moment only –30 °C. The decrease of the supercooling point in *M. kamtschatica* (by 14–19 °C) is close to that of the two above-described species, but the value of this parameter reaches only –24 °C, while the freezing point remains at its September level, which is 8 °C lower than in early summer. The supercooling point of *M. bicolor* workers is also around –24 °C, and that of the larvae of both species is –27 to –28 °C. Thus, at this stage the course of supercooling point values in *L. acervorum* and *C. herculeanus* is entirely determined by changes of their freezing point (probably resulting from increased osmotic pressure of the haemolymph due to dehydration and accumulation of carbohydrates, amino acids etc.) without considerable increases of the depth of supercooling. In contrast, in *Myrmica* the depth of supercooling changes considerably along with the freezing point: the former by 6.5 °C and the latter by 10 °C.

However, judging by the courses of the content of water, glycogen and polyols, most of the changes in cold-hardiness parameters are completed somewhat earlier, by the end of September. In late October the accumulation of polyols is already underway, and a large part of the accumulated glycogen is already used up. In adults of *C. herculeanus* some water content increase has been recorded, probably resulting from the accumulation of metabolic water produced by the synthesis of glycerol from glycogen. Such water content increases are typical of insects switching from deep diapause to oligopause (Ushatinskaya, 1973).

The increase of cold-hardiness then continues for 1–1.5 months, until early December, with temperatures in the nests –10 to –20 °C. This continuing increase is probably achieved by the synthesis of cryoprotectants. Glycerol, as was shown in *Pytho americanus* (Coleoptera), can be synthesised at very low temperatures, sometimes as low as –17 °C (Ring & Tesar, 1980). The values of the supercooling point remain constantly low from December until late April.

Winter. The lowest values of average supercooling point of all the ant species of the Upper Kolyma area were recorded in *L. acervorum*. In ants from some nests this parameter falls in the range –38.0 to –42.8 °C in workers and –33.5 to –46.4 °C in larvae, and the average value in all the nests studied in winter is –40.0 in workers and –40.2 °C in larvae. Similar degree of cold-hardiness is found in *L. muscorum* (average supercooling point –40.4±0.2 °C in workers from eight nests). As noted above, average values of supercooling point in *L. acervorum* differ between nests from areas with homogeneous temperature conditions by up to 2.5–3 °C (for workers) and are on the average 2 °C lower in the colder area. Larvae have similar values of the supercooling point, but considerably higher values of the variation coefficient within each nest (30–35%, compared to 8–16% for workers).

Low values of the supercooling point are typical also of *C. herculeanus*, but their range is somewhat narrower: –37 to –40 °C in workers and –35 to –40 °C in larvae. Males overwintering in one of the nests had in late April the same cold-hardiness (average supercooling point –32.6 °C, n = 10) as workers (–32.8 °C, n = 30). The depth of supercooling in *C. herculeanus*, as in *L. acervorum*, remains rather low all the year round and fluctuates slightly around 8 °C.

Members of the genus *Myrmica* are the least cold-hardy of all the species of this group. The values of the supercooling point of both species are close and in workers fall within the range –26.8 to –31.6 °C; in larvae they are somewhat lower, –27.6 to –33.2 °C; freezing point varies from –16 to –20 °C.

Thus, by the middle of winter, compared to late autumn (October), all the species of this group have values of freezing point decreased by 8–10 °C and virtually the same difference between supercooling point and freezing point. The

decrease of their supercooling point compared to summer values reaches 23–27 °C in *Myrmica* and 32–35 °C in *C. herculeanus* and *L. acervorum*.

The period of the greatest cold-hardiness in this group is correlated with the accumulation of large amounts of polyols: on the average up to 16% of wet biomass in adults and 22–24% in larvae of *C. herculeanus*, *L. acervorum* and *L. muscorum*. As our micro-thin-layer chromatographic analysis and gas chromatographic analysis kindly carried out by V. I. Svetashev (A. V. Zhirmunsky Institute of Marine Biology, Far Eastern Branch, Russian Academy of Sciences) showed, in the former two species polyols are represented exclusively by glycerol. In members of the genus *Myrmica* polyols are accumulated in smaller amounts, 8–12% in adults and up to 16% in larvae; gas chromatographic analysis showed that around half of the polyols is glycerol, and the other half sorbitol and mannitol.

The very strong variation in the content of polyols is caused mostly by differences in the state of ant families. For instance, the content of glycerol in two samples from the same nest was 16.2 and 18.9% in workers of *C. herculeanus* and 10.5 and 11.8% in workers of *L. acervorum*, while the results of analysis of ants from different nests differ very much in spite of considerably smaller variation in the temperature parameters of cold-hardiness: the range of polyol content is 12–19% in *C. herculeanus* and 8–22% in *L. acervorum*. Since in all the ants with different polyol contents the entire reserve of glycogen in winter is used up, all the glycogen is probably spent for the production of polyols. As for the supply of reserve substances accumulated in autumn, it depends on the combination of many factors, such as feeding or the temperature regime of the past summer.

This accumulation of large amounts of specific cryoprotectants decreasing the freezing point is observed along with still low water content, complete spending of glycogen, and glucose content as low as in autumn.

While the transitional period from summer to winter lasts 3–4 months, and cold-hardiness is increasing in the course of all this period, the transition from wintering to summer activity takes considerably less time. For instance, in late April, when the temperature in the nest of most ant species is around –10 °C, values of supercooling point as low as in February were observed, and in a month this parameter sometimes reached its highest summer values.

Emergence from overwintering is accompanied by considerable physiological and biochemical changes, resulting in the decomposition of polyols, increase of water content, and some increase of the content of glycogen. Temperature-induced glycogen/glycerol transformations have been demonstrated in many species of invertebrates (Wyatt & Meyer, 1959; Dubach et al., 1959; Chino, 1958; Wyatt, 1967; Storey & Storey, 1991). It should be noted that this clarifies the role of ice crystals filling ant tunnels in winter: after the rising of temperatures these crystals create high humidity required for the activation of ants. In

laboratory conditions ants were successfully awoken only at values of absolute humidity close to saturation.

Seasonal changes in the cold-hardiness of ants of the genus *Formica*. As mentioned above, the cold-hardiness of ants of the genus *Formica* of the Upper Kolyma area is considerably different from that described for *L. acervorum*, *C. herculeanus* and *Myrmica* spp.

Summer. The values of supercooling point vary in workers of *F. exsecta* in late May and late July from −7 to −8 to −10 to −13.5 °C, i.e. *F. exsecta* has the same range of changes as the first group of species (5–7 °C), but still lower values of the supercooling point. In *F. candida* and *F. gagatoides*, average values of the supercooling point in the first half of summer are still lower, −14 to −18 °C. Their somewhat smaller variation, compared to *F. exsecta*, may result from the smaller number of examined nests. The freezing points of this group are as high as those of the other species: from −3.5 to −7 °C (Figs. 48–50). Thus, ants of the genus *Formica* have lower values of supercooling temperature because of their greater, approximately by a factor of 1.5, depth of supercooling (on the average 10–11 °C, compared to 6–7 °C in the other species).

The physiological and biochemical parameters of *F. exsecta*, *F. candida* and *F. gagatoides* in summer represent their active state, as in the species discussed above. The content of water is around 70%, of polyols at most 0.5%, of glucose 0.5–0.7%; the only difference is the smaller glycogen content (less than 0.5%).

Autumn. The tendency to increase cold-hardiness is observed in *Formica* also starting from August, but the values of supercooling point change considerably more slowly than in the first group of species. By the end of October they reach −17.2 °C in workers of *F. exsecta*, −22.4 °C in workers of *F. candida* and −25.6 °C in workers of *F. gagatoides*, having decreased in 2–2.5 months only by 4–7 °C in each of these *Formica* species. These early autumn changes of the supercooling point result from increasing depth of supercooling, whereas the freezing point remains unchanged.

Such changes of cold-hardiness are related to the decrease of water content by 8–10%; the content of glycogen in this period is around 5% in *F. gagatoides* and *F. exsecta* and only 1% in *F. candida*. All these species display glucose accumulation, from 0.9% in *F. exsecta* to 2.5% in the other species.

The subsequent increase of cold-hardiness from November to December is also relatively small, at most 4.8 °C in *F. exsecta* and *F. gagatoides*, and still reflecting almost no changes of the freezing point.

Winter. The supercooling point has the lowest values from December to late April, as in the first group: −19.0 to −22.0 °C in workers of *F. exsecta*, −24.2 to −25.2 °C in *F. candida* and −27.2 to −30.4 °C in *F. gagatoides*. The freezing

Fig. 48. Seasonal changes of cold–hardiness (A) and carbohydrates and water content (B) in workers of *F. candida*. Other notation as in Fig. 44.

Fig. 49. Seasonal changes of cold hardiness (A) and carbohydrates and water content (B) in workers of *F. gagatoides*. Other notation as in Fig. 44.
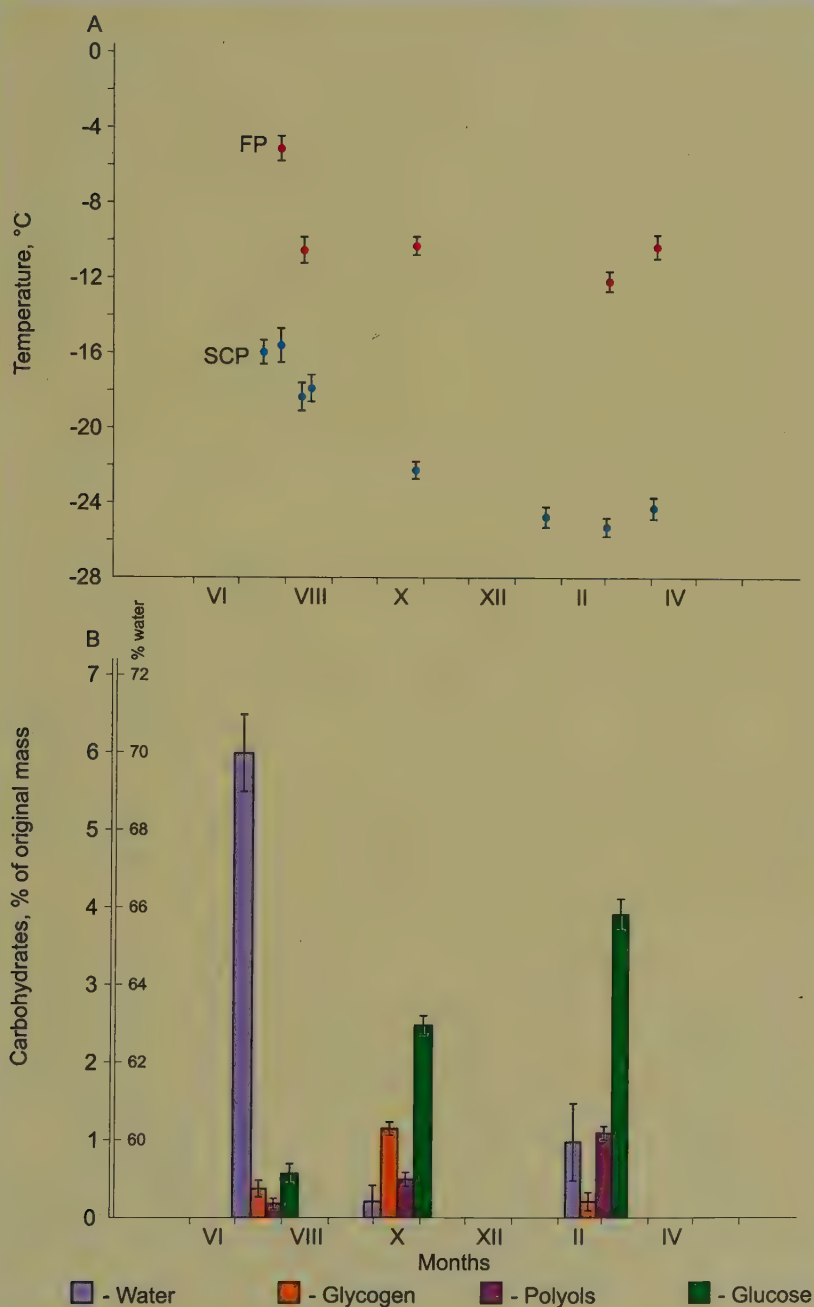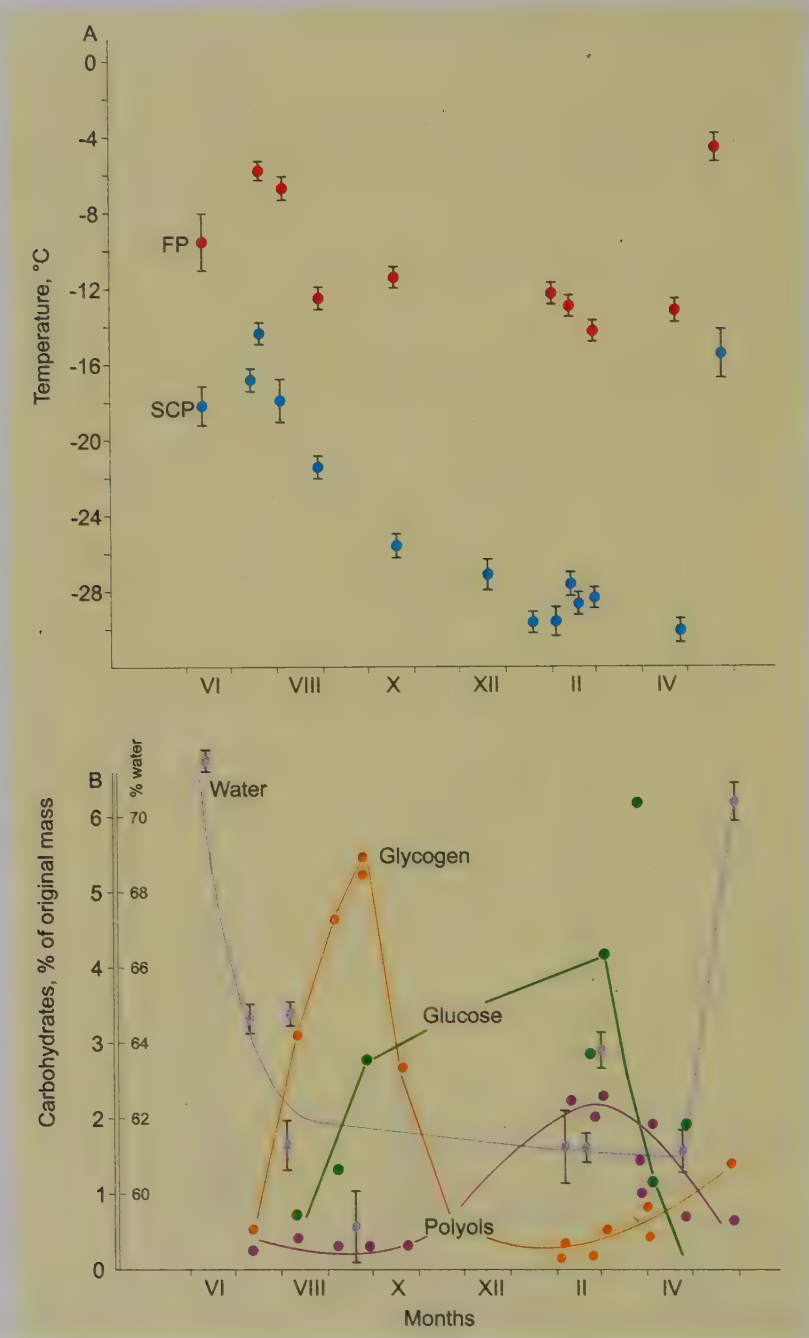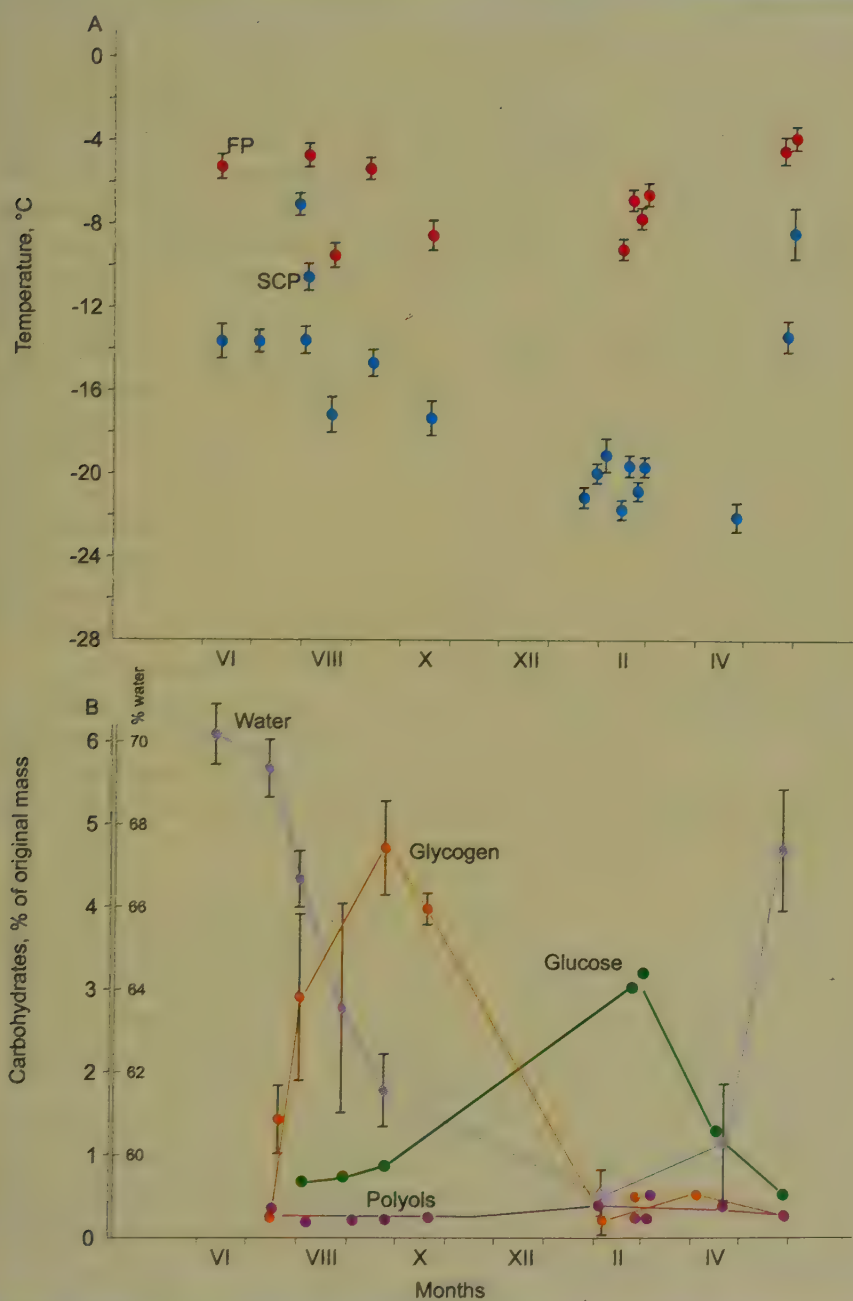
Fig. 50. Seasonal changes of cold-hardiness (A) and carbohydrates and water content (B) in workers of *F. execta*. Other notation as in Fig. 44.

point in workers of these species is −6 to −9, −10 to −12 and −12 to −14 °C, respectively.

In the period of greatest cold-hardiness the content of glucose in species of the genus *Formica* increases to 3%, and in some nests of *F. candida* even to 6%, with the content of water still low and glycogen completely used up. Generally, species of this group display relatively little cold-hardiness, and their supercooling capacity is strongly correlated with the amount of polyols. In the least cold-hardy *F. exsecta* no seasonal variation of polyol content is observed, and its value fluctuates slightly during the entire year around 0.5%. In *F. candida* the content of polyols increases to 1% in the middle of winter, and in *F. gagatoides* it reaches probably the highest value possible in this genus, 2.2%. The identification of these polyols by thin-layer chromatography has shown that in *F. gagatoides* they are represented by the poorly separable group of sorbitol, mannitol and dulcitol; glycerol was not found.

This group of species displays smaller differences of average supercooling point between ants from nests in different areas and in different years (up to around 3 °C, compared to 5 °C of the first group). As noted above, the differences between average values of the supercooling point in *F. exsecta* ants from different nests reach 3 °C, which is identical to the greatest differences between average values for ants from different chambers of the same nest.

Thus, the greatest seasonal changes of the supercooling point reach 10 °C in workers of *F. candida*, 15 °C in *F. exsecta* and 16 °C in *F. gagatoides*, which is comparable only with changes of the first (autumn) period of cold-hardiness increasing of the first group of species, and equals less than half of the entire range observed in that group.

Another typical feature of the cold-hardiness of ants from the genus *Formica* is the seasonal course of the freezing point of workers. While in the first group this parameter changes in two stages, gradually decreasing from August to September and then from November to December, in *Formica* the main changes are observed in late August and their extent is only from 6 °C in *F. exsecta* and *F. candida* to 9 °C in *F. gagatoides*, compared to 15 °C in *Myrmica* and 20–30 °C in *L. acervorum* and *C. herculeanus*.

Spring. Emergence from overwintering in *F. exsecta* and *F. gagatoides* is as rapid as in the first group of species (supercooling point and freezing point reach their highest values by the end of May) and is accompanied by the return of glucose and polyol content to their low summer levels, some increase of glycogen content, and hydration.

Characteristics of emergence from overwintering in different species. To determine the rate of emergence from overwintering in ants of both groups

and the factors determining this rate, we tried in early May to imitate prolonged spring. With this purpose, we covered plots of soil 4–5 m² containing several nests of *F. gagatoides*, *M. kamtschatica* and *L. acervorum* in a moss–dwarf-shrub larch forest with felt mats to prevent them from thawing. The temperature at that moment was –3 °C at the depth of 5 cm and around –5 to –6 °C at the depth of 15 cm in the tussock. The nests remained under their felt cover, with temperatures gradually increasing, until May 22, when they were excavated, and the supercooling points of ants were measured. The temperature in the nests with transitional period artificially prolonged by 20 days was at most –1 to –2 °C at the moment of excavation, while in natural conditions it already reached 5–10 °C. Comparison of supercooling point values of ants from artificially prolonged transitional period and from nests with natural temperature regime shows that the spring decrease of cold-hardiness is caused by the increase of temperatures to negative values close to zero.

The greatest increase of the supercooling point in the experimental group of ants was observed in *L. acervorum*: by 13 °C; and it was caused exclusively by the increase of the freezing point (Table 14), which indicates the decomposition of polyols. In control nests of this species positioned in tussocks of different size and humidity, temperatures differed considerably, which was reflected in the wide range of cold-hardiness parameters: in workers of *L. acervorum* the values of the supercooling point varied from –9 to –18 °C.

In the course of exposure to freezing temperatures close to zero, the supercooling point of *M. kamtschatica* workers increased by 10.5 °C, and their freezing point increased by 8.5 °C, while in nests with a natural temperature

Table 14. Temperature parameters (°C) of the cold-hardiness of ants from the nests with different temperature regime, excavated on 22–26 May 1979

Species	Temperature in the nest	Supercooling point of crop m ± SE	Supercooling point of tissues m ± SE	Freezing point of tissues m ± SE	Supercooling of tissues m ± SE	Number of individuals (n)
F. gagatoides	–2	–10.7±0.4	–26.0±0.7	–10.3±0.6	15.8±0.6	23
F. gagatoides	5	–9.5±1.3	15.7±1.3	–4.8±0.4	11.0±1.0	27
M. kamtschatika	–2	–8.9±0.2	–20.8±1.5	–11.8±1.1	9.1±0.6	21
M. kamtschatika	5	–7.6±0.4	–10.1±0.5	–5.3±0.4	4.8±0.4	22
L. acervorum	–2	–16.1±1.1	–27.6±0.9	–17.8±0.8	9.7±0.6	25
L. acervorum	1	–12.0±0.7	–18.2±0.8	–7.7±0.4	10.5±0.6	24
L. acervorum	10	–7.6±0.3	–9.4±0.6	–3.6±0.4	5.7±0.4	11

regime these parameters reached their summer values during the same time period (see Table 14). Considerably smaller changes after exposure to freezing temperatures close to zero in the course of an artificially prolonged transitional period were observed in adults of *F. gagatoides*, the supercooling point of which was raised by 4 °C, mostly because of an increased freezing point. Thus, in all the studied species of ants the rise of temperature in the nest to values close to zero results in decreasing cold-hardiness. The range of these changes is different in different groups of species and evidently reflects the starting biochemical reorganization prior to activation.

Ants awaking from overwintering after exposure to room temperature in winter require for the renewal of locomotor activity from several minutes to half an hour in *F. exsecta* and 12–24 hours in *F. gagatoides*. Individuals of *L. acervorum* and *M. kamtschatica* awake no sooner than after 24 hours, and individuals of *C. herculeanus* awake after 3–5 days. The courses of polyol decomposition in ants exposed in January to room temperature fully agree with the courses of their awakening (Table 15).

All these conclusions on the rate of spring transitional processes in ants were confirmed by another laboratory experiment. A nest of *L. acervorum* excavated in mid-March was divided into two parts, and one part was placed in a controlled-temperature chamber at −5 °C, while the other part remained at room temperature. After 10 days of exposure, cold-hardiness parameters were measured in ants from both parts of the nest. The average supercooling point of 26 workers exposed to the temperature −5 °C was −30 °C (while normally the winter values of supercooling point in this species are around −40 °C), whereas in 27 individuals exposed to room temperature this parameter was only −9.0 °C. Thus, the period of 10 days was sufficient for the ants to complete their transitional processes. Probably this period could be even shorter, but we have no data to confirm this.

These results lead to an important methodological conclusion. In studies of extreme values of cold-hardiness parameters or their seasonal courses, all the measurements should be taken as soon as possible. Even brief keeping of

Table 15. Polyol content in overwintering and awaking ants (% wet mass)

Species	Wintering ants	Ants awaking from wintering			
		1st day	2nd day	3rd day	30th day
C. herculeanus	16.2	–	7	0.6	0.3
M. kamtschatica	10	–	1.6	0.7	0.4
F. gagatoides	0.9	0.5	0.3	0.3	0.3

Note. "–", no data.

animals in conditions different from natural is not acceptable. In our study area or in any other area with continuous permafrost and anticyclonic type of winter weather, brief (1–3 days) keeping of ants taken from excavated nests in winter is possible only at temperatures around –10 °C for all the species.

<p style="text-align:center">*   *   *</p>

To summarize all the above-given data on the cold-hardiness of ants, estimated by supercooling point, and the mechanisms providing their cold-hardiness, let us single out the principal patterns of the seasonal variation of this parameter. The supercooling points of ants inhabiting the Upper Kolyma area form an almost continuous series, from the most cold-hardy *L. acervorum* and *C. herculeanus* (average supercooling point –38 to –43 and –37 to –40 °C, respectively) to the less cold-hardy species of the genus *Myrmica* (–27 to –32 °C) and *F. gagatoides* (–27 to –30 °C) and the most cold-sensitive *F. candida* (–24 to –25 °C), *F. lemani* (–20 to –24 °C), *F. exsecta* (–19 to –22 °C) and *F. sanguinea* (–17 to –18 °C). The values of the supercooling point observed in some individuals of the most cold-hardy species are close to record values of this parameter known in insects.

The studied species can be divided into two groups on the basis of the seasonal variation type of their temperature parameters of cold-hardiness. In the first group (*L. acervorum*, *L. muscorum*, *C. herculeanus*, *M. kamtschatica* and *M. bicolor*) values of supercooling point change from summer to winter by up to 25–30 °C, mostly because of decreasing freezing point, whereas in the second group (the genus *Formica*) this parameter changes by 6–12 °C, and mostly because of increasing depth of supercooling (freezing point changes by only 1–6 °C).

The mechanisms providing winter cold-hardiness in the two groups are different in a similar way. In the first group (*L. acervorum*, *L. muscorum*, *C. herculeanus*, *M. kamtschatica* and *M. bicolor*) cold-hardiness is provided by accumulation of considerable amounts of polyols, used as antifreeze. The second group, including only species of the genus *Formica*, is less cold-hardy, and the increase of their cold-hardiness from summer to winter is provided mostly by increasing supercooling capacity with more or less unchanging values of the freezing point and almost complete absence of antifreeze substances. However, in spite of such different mechanisms of providing winter cold-hardiness in different species, the achieved effect (judging by supercooling point) is virtually identical. The most striking examples are *M. kamtschatica*, with its distinct biochemical adaptations, and *F. gagatoides*, which is generally believed to have no such adaptations (Kipyatkov, 1981; Maavara, 1983).

The temperature parameters of cold-hardiness display considerable variation both in summer and in winter. Values of the supercooling point of most individuals in each nest are distributed over a wide range, around 15–20 °C in species of the genus *Formica* and 12–15 °C in other species. This variation in the

cold-hardiness of individuals from the same nest is evidence to the heterogeneity of populations and probably reflects the extreme environmental conditions of ants in Northeastern Asia. But this cannot be stated with certainty in the absence of similar data from central parts of the ranges of these ants.

RESISTANCE OF ANTS TO LONG-TERM EXPOSURE TO SUB-ZERO TEMPERATURES

Estimation of the relation of insects to their overwintering conditions requires determination not only of their capacity of surviving short-term exposure to low temperatures, but also their resistance to long-term effects of cold, i.e. the lowest long-term tolerable temperatures, and comparing them with supercooling points. We determined the dependence of ant mortality on the duration of exposure (within the range from 15 minutes to 3 days) to sub-zero temperatures differing by 2–10 °C from the average values of supercooling point.

Dependence of ant mortality on duration of exposure. As mentioned above, the formation of ice in the body of frost-avoiding insects, which overwinter in a supercooled state, is invariably lethal to them. However, the crystallization of water is not the only cause of their death. Even without the freezing of water, irreversible changes in the nervous system are possible, leading to paralysis and death in distant future, sometimes after several months (Rasnitsyn, 1963). In estimations of the impact of cold, especially in experiments with freeze-tolerant species, individuals displaying incoordination of movements are also considered unable to survive the temperature to which they were exposed. The causes of low-temperature damage unrelated to freezing are discussed in detail by many authors (see Denlinger & Lee, 1998).

The dependence of the mortality of freeze-avoiding insects on the duration of exposure to low temperatures has been studied in a number of species: *Cephys cinctus* (Hymenoptera, Cephidae) (Salt, 1966c); *Pieris brassicae* (Lepidoptera, Pieridae), *Apanteles glomeratus* L. (Hymenoptera, Braconidae) (Merivee, 1972, 1978); *Petrova resinella* (Lepidoptera, Tortricidae) (Kuusik, 1970); *Formica aquilonia* (Hymenoptera, Formicidae) (Maavara, 1983). These works have shown that linear dependence of mortality on the logarithm of exposure duration is observed in the interval from 15 minutes to 24 hours (Merivee, 1972). The same dependence was observed by R. Salt (1966c) at considerably longer durations of exposure, up to several months. At temperatures 5.5–6.5 °C higher than supercooling point the probability of death from cold is decreased almost to zero (Merivee, 1972).

We also observed linear dependence of the proportion of killed ants on the logarithm of duration (Fig. 51). The change of temperatures to which ants are exposed from 0 to −14 to −30 °C cannot be instant and requires usually 0.5 to 2 hours. This cooling period results in the freezing of all the individuals with supercooling points higher than the temperature in the chamber. The
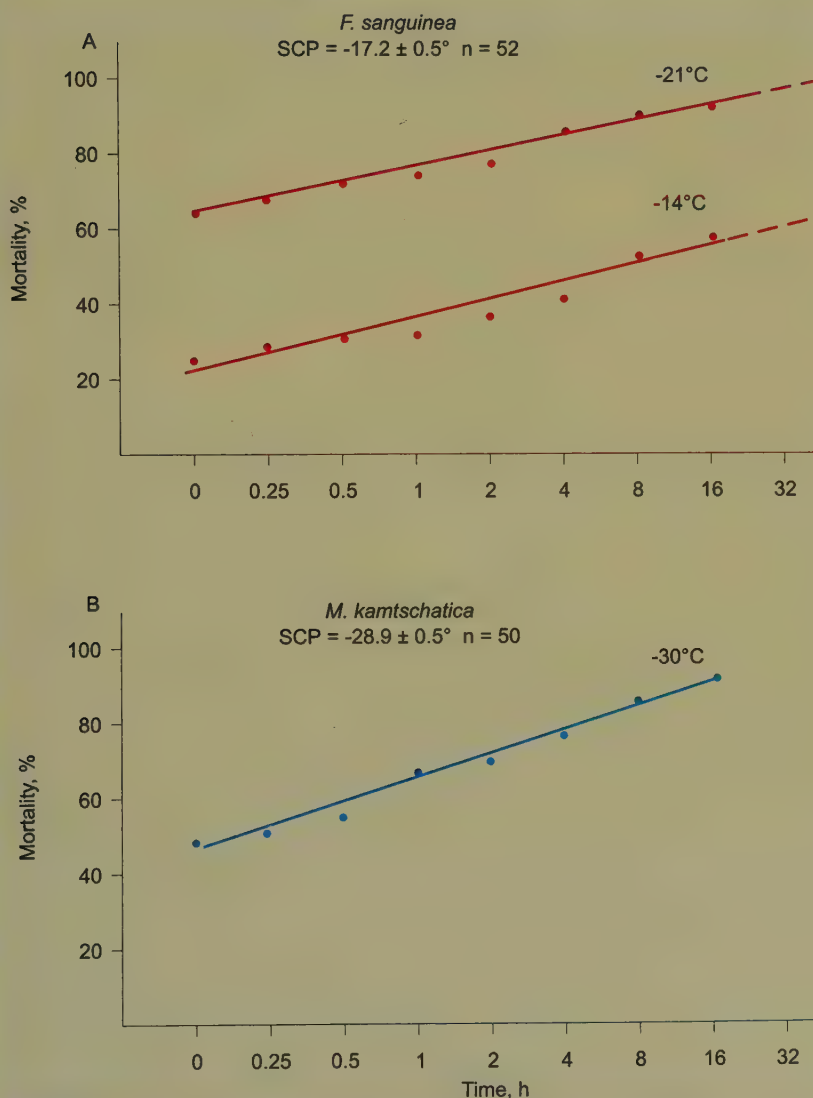

Fig. 51. Dependence of mortality on duration of exposure to low temperatures in workers of *F. sanguinea* (A) and *M. kamtschatica* (B).

subsequent freezing of individual ants should be best considered resulting from the probabilistic process of ice nucleators formation, not caused by increases of the supercooling point with time. Naturally, at lower temperatures ants are exposed on the average to greater degrees of supercooling, and the probability of spontaneous crystallization of their supercooled liquids is higher. This effect is probably reflected in the steeper gradient of the regression line representing the dependence of mortality on exposure duration at lower values of temperature (Merivee, 1972, 1978). The realization of linear dependence of mortality on the logarithm of exposure duration implies small differences between the values of mortality after long exposure to cold, from 24 hours to several weeks and even months (Salt, 1966c; Merivee, 1972, 1978).

In our case of ants overwintering in the soil, where the temperature changes show both considerable time lags and reduced amplitude compared with those of the surface, exposure duration of 1–3 days is important, comparable to the duration of periods when lowest values of temperature are usually observed. Therefore, we focused on determining the mortality of ants after relatively long exposure to low temperatures, for 24–30 hours.

Dependence of ant mortality on temperature under long-term exposure. The temperature causing the death of 50% of individuals after 24-hour exposure is an accepted measure of resistance to cold in freeze-tolerant species (Ring, 1982). Similarly, and in accordance with the conclusions explained above, we used the same parameter, $LT_{50\%}$, to characterise the resistance of ants to long-term exposure to low temperatures. Thus, our principal objective was determining the lowest values of temperatures survived by ants in winter ($LT_{50\%}$) and comparing them with the values of the supercooling point, for subsequently estimating the probable winter mortality of ants in nature.

We studied these parameters in all the ant species abundant in the Upper Kolyma area, except *F. candida* and *C. herculeanus*. In additions, since in the literature active (summer) insects were reported to be incapable of surviving even negative temperatures close to zero, in spite of relatively low supercooling points (Ushatinskaya, 1980), in some species we also determined the lowest temperatures tolerable in summer.

The temperature resulting in 50% mortality in wintering *F. exsecta* ants from two nests with average supercooling point −17.6±0.6 and −21.6±0.6 °C was −11.5 and −14 °C, respectively (Fig. 52). Thus, long-term exposure to temperatures higher by 6–7 °C than supercooling point is lethal to ants of this species. Surprisingly, in summer this difference also equals 6–7 °C, allowing workers of *F. exsecta* to survive in summer experiments at temperatures as low as −8 °C. Such cold-hardiness in summer is clearly redundant, and should be considered

Fig. 52. Distribution of supercooling points (A) and dependence of mortality after 24-hour exposure to low temperatures on temperature (B) in winter and in summer in workers of *F. exsecta*. Figures hereinafter indicate sample size in each group and average supercooling points with mean error.

non-specific, since even at the surface of the soil such severe freezing has not been recorded in our study area in summer. Taking into account that the freezing point of *F. exsecta* in summer falls within the range –6 to –7 °C and in winter is only 2–3 °C lower, we may conclude that in summer this species normally does not experience supercooling, whereas the supercooling it experiences in winter is very strong. It should be noted that these speculations hold true even considering the fact that the measured values of freezing temperature are admittedly lower than its true values (see Methods).

Two other species of the genus *Formica* with high winter values of the supercooling point display patterns similar to that of *F. exsecta*. While the average supercooling point in workers of *F. sanguinea* is –17.2 °C, the death of half of the individuals is observed at –11.5 °C (Fig. 53), which is almost 6 °C higher than the average supercooling point and 4.5 °C lower than the average freezing point (–7.1±0.3 °C). The summer $LT_{50\%}$ of this species was not determined, but it is no higher than –8 °C, at which temperature the death of only 26% of the individuals was observed. Workers of *F. lemani* are supercooled on the average to –21.4 °C, and their lowest long-term tolerable temperature is –14 °C (7.5 °C higher than supercooling point and 4.5 °C lower than freezing point). The

Fig. 53. Distribution of supercooling points (A) and dependence of mortality after 24-hour exposure to low temperatures on temperature (B) in winter and in summer in workers of *F. sanguinea* and *F. lemani*.

summer $LT_{50\%}$ of *F. lemani* workers is equal to their average freezing point, −8 °C, which is 7 °C higher than their average supercooling point.

It is interesting to compare the cold-hardiness parameters of *F. gagatoides* workers from nests of *F. sanguinea*, where they are kept as "slaves", and their own nests. The average supercooling points of these samples differ considerably: −21.1 and −28.4 °C, respectively (Figs. 54, 55), which may indicate the less suitable conditions for this species in *F. sanguinea* nests. However, in both cases $LT_{50\%}$ is less different from average supercooling point than in all the species discussed above. This parameter equals −17.5 °C in "slaves" (difference from supercooling point 3.5 °C) and −27.2 °C in "free" workers, i.e. only 1.3 °C higher than the average supercooling point and 12.5 °C lower than the average freezing point. Even if the lowest long-tolerable temperatures of *F. gagatoides* are somewhat underestimated due to insufficient sample size (as mentioned above, at least 50 individuals are exposed to each value of low temperature), such a considerable stability of the state of deep supercooling at a postembryonic stage is remarkable by itself. Higher temperature parameters of cold-hardiness observed in *F. gagatoides* "slaves" are, on the one hand, doubtlessly warranted by the temperature conditions of their wintering: nests of *F. sanguinea* are found only in warm
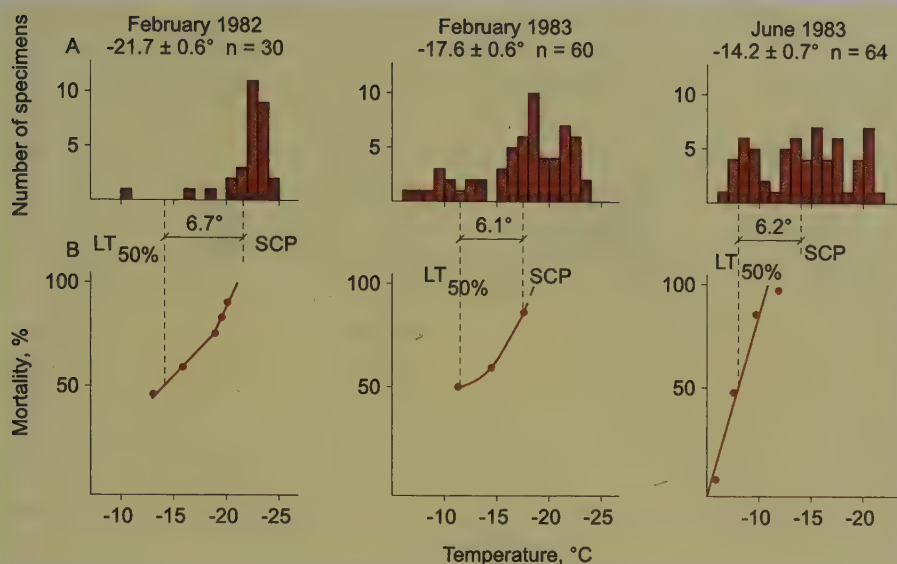

Fig. 54. Distribution of supercooling points (A) and dependence of mortality after 24-hour exposure to low temperatures on temperature (B) in winter and in summer in workers of *F. gagatoides* (slaves) from a nest of *F. sanguinea*.

Fig. 55. Distribution of supercooling points (A) and dependence of mortality after 24-hour exposure to low temperatures on temperature (B) in winter and in summer in workers of *F. gagatoides*.

areas. On the other hand, these higher values may reflect the less suitable living conditions for this species in *F. sanguinea* nests, which result in smaller amounts of reserve substances accumulated by "slaves", compared to "free" workers. A similar phenomenon was observed in the nests of *F. aguilonia*, where two groups of workers were recognized, differing in their supply of reserve substances, which depended on their functions in the nest (Hansen & Viik, 1981b). In summer, at low values of supercooling point, typical to *F. gagatoides* (around −18 °C), their lowest long-tolerable temperature is −9 °C, which is considerably higher than supercooling point, but still 1.5–2.5 °C lower than freezing point.

The average supercooling points of both *Myrmica* species are close to those of *F. gagatoides*. In the nests of *M. kamtschatica* and *M. bicolor* we examined, the average supercooling point was −28.9 and −30.1 °C and the lowest long-term tolerable temperature −26.5 and −25.5 °C, respectively (Fig. 56). The freezing points of these ants were around −18 °C; further decrease of temperatures by 6–9 °C proves lethal to them. The summer values of lowest long-term tolerable temperature of these species were not determined.

Determining the lowest long-term tolerable temperature in *L. acervorum* was a difficult task. Due to the small number of individuals in its nests, it was impossible to take from a single nest a sample of sufficient size for determining
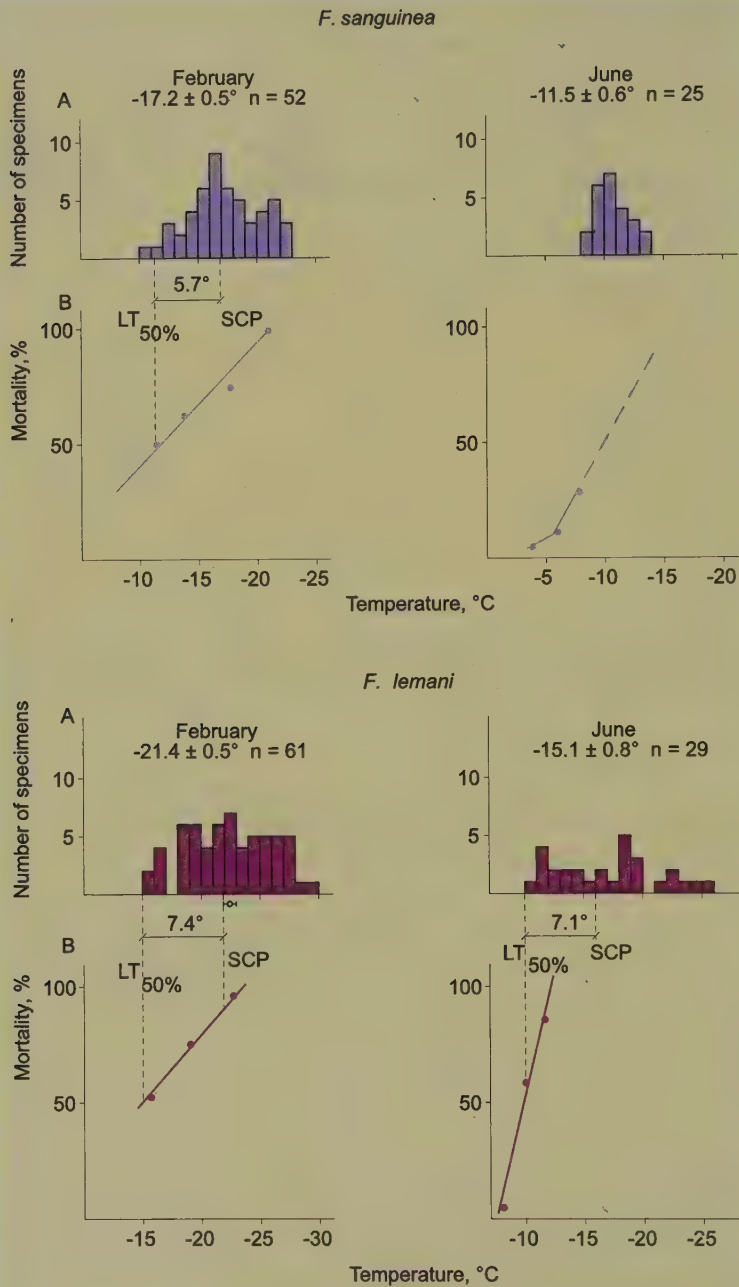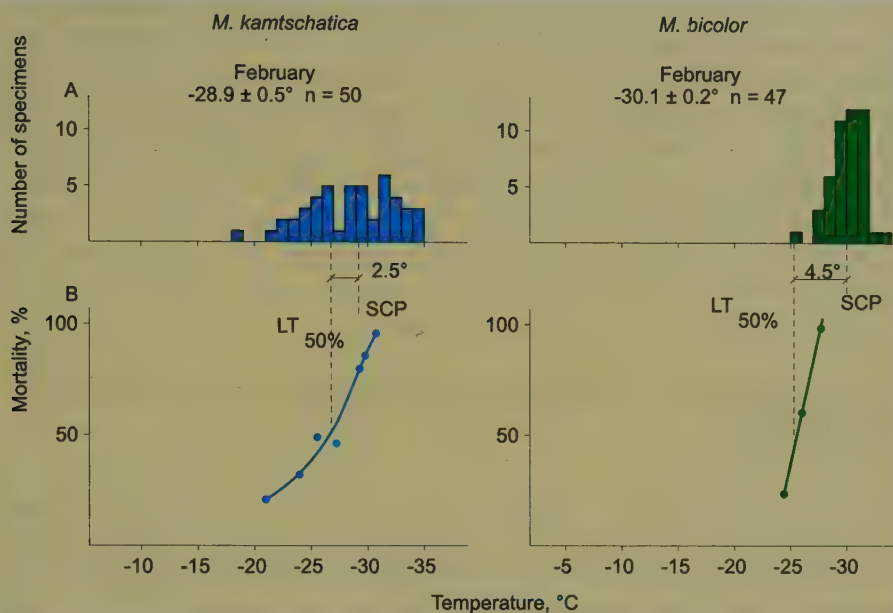
Fig. 56. Distribution of supercooling points (A) and dependence of mortality after 24-hour exposure to low temperatures on temperature (B) in winter in workers of *M. kamtschatica* and *M. bicolor*.
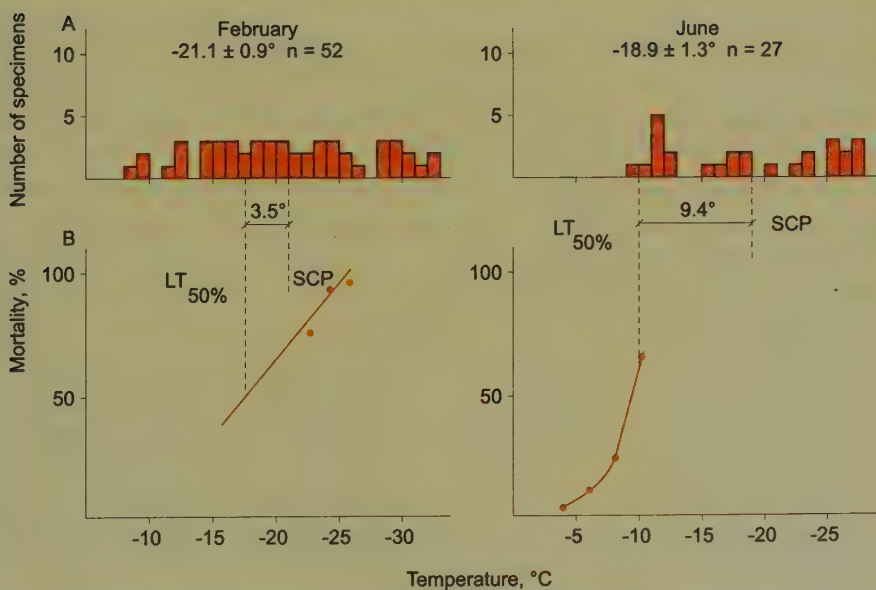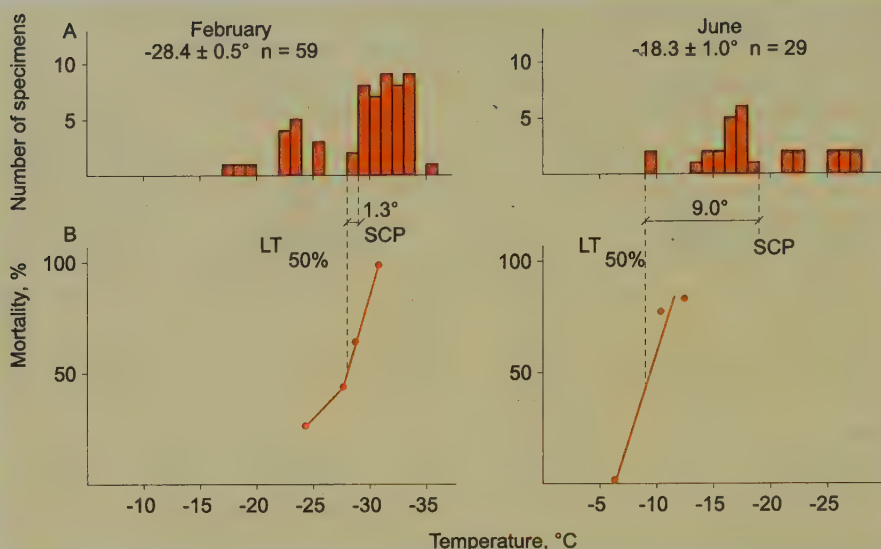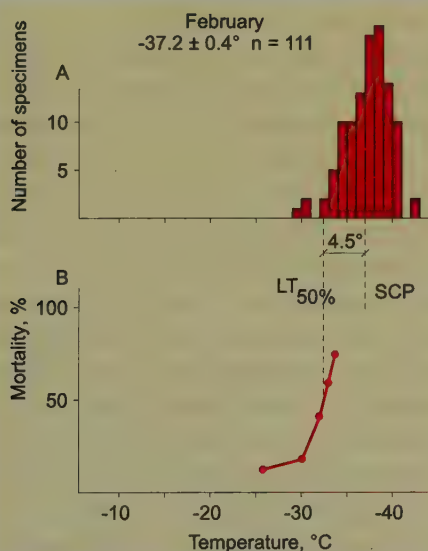

Fig. 57. Distribution of supercooling points (A) and dependence of mortality after 24-hour exposure to low temperatures on temperature (B) in winter in workers of *L. acervorum*.

both the average supercooling point and the lowest long-term tolerable temperature. Therefore, we used in this study data from three nests with different average values of the supercooling point. Mortality at 1–2 temperatures differing from the supercooling point by 5–10 °C was determined in ants from each nest. The results of these experiments were combined (Fig. 57). The values of the lowest long-tolerable temperatures determined in this way are 3–5 °C higher than the supercooling point. Taking into account the depth of supercooling, as low as 8–10 °C in workers of *L. acervorum*, long exposure to temperatures more than 5 °C lower than their freezing point is lethal to them.

COLD-HARDINESS OF ANTS FROM DIFFERENT GEOGRAPHICAL POPULATIONS

The above-described picture of the cold-hardiness of ants living in very harsh climatic conditions naturally poses the question of the cold-hardiness of the same species in areas with only moderately cold winters. In other words, it is interesting to study the formation of cold-hardiness in a species with increasing harshness of climatic conditions.

However, comparison of the cold-hardiness of insects from different geographical populations is a very difficult task. Considerable physiological diversity of individuals, typical of natural populations of insects (Ushatinskaya, 1987), while being an important adaptation contributing to the preservation of species in variable environmental conditions, at the same time creates certain difficulties for correct comparison of data from different geographical areas. As shown above, the distributions of individuals with different values of cold-hardiness parameters are usually fairly diverse even within the same nests (in different chambers), and the more so in different nests from the same area. Only very large samples from many nests can provide values of cold-hardiness parameters constant for a particular territory, as it was done with *F. exsecta* (Berman et al., 1984). Unfortunately, this approach is extremely labour-consuming.

Data on *L. acervorum* from the environs of the Aborigen Station show that the ranges of cold-hardiness in workers found in a substantial sample (30–40 individuals) from large nests are quite densely filled with intermediate average values, if a sufficient number of nests are studied (Fig. 58). Therefore, a possible simplified, estimating approach to comparing the cold-hardiness of ants from different geographical population is using the lowest average values recorded in different nests, as well as the lowest values of the supercooling point of individuals. This approach is justified if harsher temperature conditions can shift the
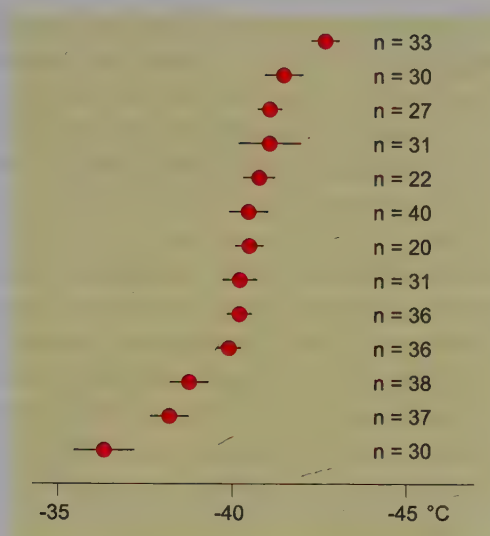
Fig. 58. Range of average supercooling points in workers of *L. acervorum* from 13 nests (1981, Aborigen).

cold-hardiness parameters of a large part of the ants in a nest to values close to the lowest recorded in the nest at relatively high temperatures.

Unfortunately, few publications on the cold-hardiness of insects taken in winter from natural conditions of different geographical areas are available. Average values of supercooling point can be influenced by a number of factors, including stochastic ones. This is why in a recent review of the data on cold-hardiness of insects dwelling in different climates (Turnock & Fields, 2005) only differences greater than 4 °C were accepted as evidence of actual difference between species or populations. The average supercooling point in most of freeze-avoiding species slightly varies within their geographic range. Differences in supercooling point greater than 4 °C were found in 15 of the 25 species for which data on the cold-hardiness of two or more geographic populations are available, and differences greater than 10 °C were found in 5 species. Correlation between differences in supercooling point and temperature conditions of the environment was found only in 4 species. The adequacy of cold-hardiness to environmental conditions was demonstrated in only one work known to us, on the ant *L. acervorum* (Heinze et al., 1998). But the authors of that work studied only tolerable temperatures, clearly undervaluing the importance of supercooling points, for which reason it is, unfortunately, impossible to compare their data with ours. All this considered, there are reasons to believe that the question of the adequacy of cold-hardiness of geographically remote populations and their wintering conditions has not been sufficiently studied so far.

Having at our disposal a vast array of data on the cold-hardiness of the abundant ant species of the Northeast of Asia, we carried out comparative studies of the cold-hardiness of ants dwelling in areas with milder climate: near Magadan (where the warming influence of the sea has visible effect) and in southern Finland (Tvärminne, at northwestern coast of the Gulf of Finland, 59°50' N, 23°15' E) and northern Finland (Kevo, 69°50' N, 27° E).

Overwintering conditions of ants in the environs Tvärminne, Kevo and Magadan. Seemingly, the best conditions are enjoyed by ants in Tvärminne (Table 16), where winter is most mild. The average temperature of February in this area is only −6.0 °C; the average annual minimum temperature is, however, relatively low, −21.3 °C (Pantyukhov, 1964). Soil temperatures in Tvärminne were not measured; the nearest site of long-term monitoring, the Jokioinen Weather Station, is situated east of Tvärminne and, more importantly, in 60 km from the sea, which results both in lower average air temperatures and greater thickness of the snow cover (48 cm, compared to 18 cm in Tvärminne, where much of the snow is quickly melting). But even in Jokioinen soil temperatures

Table 16. Air and soil temperatures of the studied geographical localities

Locality (meteorological station)	Average		Lowest soil temperature (°C) at depth			
	snow cover depth, cm	air temperature (°C) of January	0 cm	5 cm	20 cm	50 cm
Oymyakon (Agayakan)	37	−50.0	−25.0	−24.7	−22.8	−21.0
Aborigen (Detrin)	40	−37.8	−18.0 to −43.0	−17.0 to −40.0	−16.0 to −38.0	−10.0 to −15.0
Magadan (Nagayeva)	60	−18.2	−17.0 to −30.4	−9.0 to −18.5	−5.3 to −15.7	−3.5 to −6.5
Kevo (Itsujoki)	67	−14.1	−4.0 (−7.0)	−3.5 (−6.07?)	−3.1 (−5.1)	−1.4 (−3.4)
Jokioinen (same name)	48	−7.4	−1.0 (−7.2)	−0.7 (−6.6?)	−0.3 (−2.8)	+0.4 (−0.5)
Tvärminne (same name)	18	−6.0	−	−	−	−

Note. Values of soil temperatues are: the lowest of measured once in every 10 days for Agayakan (Berman et al., 1982), ranges of temperatues in biotopes with different snow depth for Aborigen and environs of Magadan (Berman et al., 1984, 1987, 1990), lowest average monthly and absolute long-term minimum (in brackets) for Kevo and Jokioinen (Results..., 1979); "?" data obtained by interpolation; "−", no data.

are high: the lowest average monthly value is −1.0 °C even at the surface of the soil, and the absolute minimum is −7.2 °C (−6.6 °C at the depth of 5 cm and −0.8 °C at the depth of 20 cm). However, in Tvärminne, in contrast to Jokioinen, the snow cover is formed and melted several times each winter. Over the period from 1963 to 1974, in 40% of the years the thickness of the snow cover on the last day of the winter months (October–March) was no greater than 5 cm, and in 25% of the years snow cover was totally absent (Climatological..., 1979), while air temperatures sometimes fell as low as −22 °C even in early March. It is clear that these values of soil temperatures are in any case higher than the temperature parameters of cold-hardiness in the ants of Tvärminne (Tables 17–19). However, falls of temperature in March usually happen between periods with positive temperatures and soil already thawed, without snow cover. Ants occupying nests with surface position of chambers are exposed to "spring" conditions, their cold-hardiness decreases, and abrupt deep falls of temperature

Table 17. Cold-hardiness (°C) of *L. muscorum* in different studied localities of its range

Locality	Date of measuring	Supercooling point			Freezing point		Supercooling	
		m ± SE	min	n	m ± SE	n	m ± SE	n
Adults								
Summer								
Oymyakon	9.VII.79	−13.1±0.4	−15.4	15	−9.7±0.3	15	3.5±0.2	15
Winter								
Tvärminne	8.III.91	−22.9±1.0	−29.0	33	–		–	
	21.II.92	−25.4±0.4	−29.6	44	−21.5±0.7	21	3.9	
	21.II.92	−27.4±0.5	−31.0	54	−23.9±0.5	43	3.5	
Oymyakon	30.III.80	−36.7±0.0	−43.4	27	−30.6±0.9	27	6.0±0.2	27
	29.III.80	−44.2±0.8	−47.0	12	−39.6±1.0	11	4.6±0.3	11
Larvae								
Summer								
Oymyakon	9.VII.79	−9.5±0.4	−14.2	25	−6.6±0.3	25	2.9±0.3	25
Winter								
Tvärminne	21.II.92	−23.3±0.5	−28.4	35	−19.1±0.8	12	4.2	
	21.II.92	−23.9±0.5	−30.1	43	–		–	
Oymyakon	30.III.80	−31.6±1.7	−45.3	11	−30.7±1.6	11	1.0±0.2	11
	28.III.80	−44.1±0.9	−58.1	41	−43.0±1.0	41	1.1±0.1	41

Note. From summer data on Oymyakon, lowest of average supercooling points are given, with corresponding freezing points and supercooling; from winter data, lowest and highest values are given; "m ± SE", mean ± standard error; "min", lowest value in a sample; "n", sample size; "–", no data.

may result in the freezing of awoken individuals. Thus, the winter climate of Tvärminne is not so mild towards insects wintering in surface layers of the soil without snow cover. Abrupt falls of temperature, especially short-term, are no less dangerous than constantly low temperatures, and it is these abrupt falls that probably require "redundant" cold-hardiness.

In the environs of Kevo, a typical northern Finland area, ants overwinter in fundamentally different conditions. The average air temperature of February (the

Table 18. Cold-hardiness (°C) of *L. acervorum* from different studied localities of its range

Locality	Date of measuring	Supercooling point			Freezing point		Supercooling	
		m ± SE	min	n	m ± SE	n	m ± SE	n
Adults								
Summer								
Aborigen	27.VII.78	−12.4±0.4	−14.9	17	−9.9±0.3	17	2.5±0.3	17
Winter								
Kevo	26.II.92	−22.9±0.6	−28.5	44	−15.9±0.8	42	7.0	
	27.II.92	−27.1±0.3	−31.5	46	−21.8±0.7	53	5.3	
Tvärminne	7.III.91	−22.3±1.0	−29.1	33	−		−	
	19.II.92	−25.6±0.6	−30.9	42	−		−	
	5.III.91	−26.7±0.45	−29.5	31	−		−	
Magadan	13.IV.92	−22.8±0.6	−31.8	49	−15.5±0.6	49	7.3	
	6.IV.92	−25.6±1.0	−32.4	27	−19.1±1.0	27	6.5	
Aborigen	27.II.81	−36.3±0.8	−43.1	30	−26.4±0.8	30	9.8±0.3	30
	18.II.92	−42.7±0.3	−47.6	33	−35.4±0.4	33	7.1±0.2	33
Larvae								
Summer								
Aborigen	25.VII.78	−11.1±0.2	−13.2	29	−6.1±0.3	29	5.0±0.2	29
	8.VII.79	−9.6±0.3	−12.8	25	−6.6±0.4	25	3.0±0.2	25
	13.VII.78	−11.6±0.3	−13.2	18	−6.8±0.4	18	4.8±0.4	18
Winter								
Kevo	27.II.92	−18.3±0.5	−27.0	49	−13.3±0.6	46	5.0	46
	27.II.92	−25.4±0.8	−37.3	47	−22.1±0.9	28	3.3	
	29.II.92	−23.4±0.6	−32.1	42	−21.5±0.7	33	1.9	
Tvärminne	5.III.91	−22.4±0.4	−26.9	54	−		−	
	20.II.92	−27.0±0.8	−35.0	49	−		−	
Magadan	13.IV.92	−24.6±0.6	−34.0	52	−21.8±0.6	52	2.8	52
	10.IV.92	−25.7±1.4	−34.0	26	−23.6±1.5	26	2.1±0.2	26
Aborigen	28.II.81	−35.4±0.5	−39.9	37	−33.3±0.5	37	2.1±0.1	37
	25.X.78	−48.2±2.3	−56.1	11	−		−	

coldest month of the year) is −14.1 °C, the average annual minimum temperature is −33 °C. However, with average thickness of the snow cover (during the period of largest accumulation of snow) 67 cm, the temperature at the surface of the soil never drops lower than −7.0 °C (absolute annual minimum), with the average value −4.0 °C (Results…, 1979). In areas somewhat south of Kevo and, thus, more continental, at the Sodankylä Weather Station, the absolute minimum soil temperatures in all of Finland were recorded (over the period from 1963 to 1970), which were, however, no lower than −11 °C in the upper cm of the soil. These data indicate quite favourable conditions for the overwintering of *L. acervorum*

Table 19. Cold-hardiness (°C) of workers in nests of *F. exsecta*, *F. gagatoides* and *F. lemani* from different studied localities within their ranges

Locality	Date of measuring	Supercooling point		Freezing point	Supercooling	
		m ± SE	min	m ± SE	m± SE	n
F. gagatoides						
Summer						
Aborigen	6.VI.83	−18.9±1.3	−27.9	−5.8±0.5	13.1±1.0	27
Winter						
Kevo	28.II.92	−19.4±0.5	−25.5	−10.1±0.6	9.3±0.5	50
Magadan	16.IV.92	−21.5±0.5	−26.0	−9.5±0.5	12.0±0.5	46
Aborigen	25.II.81	−27.5±0.5	−33.1	−13.0±0.4	14.6±0.4	40
	25.IV.79	−30.3±0.5	−32.5	−13.1±0.4	17.2±0.5	20
F. lemani						
Summer						
Aborigen	6.VI.83	−15.1±0.8	−23.9	−5.2±0.4	10.3±0.7	29
Winter						
Kevo	1.III.92	−16.2±0.5	−22.8	−9.2±0.5	7.0±0.5	42
Magadan	7.I.94	−14.7±0.6	−22.1	−6.6±0.3	8.0±0.5	45
Aborigen	7.IV.83	−20.7±0.5	−28.2	−9.4±0.2	12.3±0.4	66
	31.III.83	−26.7±0.6	−32.4	−13.9±0.4	12.6±0.4	39
F. exsecta						
Summer						
Aborigen	6.VI.83	−14.9±0.7	−21.6	−5.2±0.5	9.7±0.5	32
Winter						
Tvärminne	8.III.91	−10.7±0.7	−18.8	−5.4±0.2	5.7±0.3	41
Kevo	28.II.92	−15.9±0.3	−20.4	−8.8±0.5	7.2±0.5	46
Magadan	8.I.94	−15.4±0.4	−20.1	−7.2±0.2	8.2±0.3	52
Aborigen	2.III.92	−18.6±0.9	−26.8	−6.9±0.4	11.7±0.7	33
	25.II.92	−22.5±0.3	−24.5	−8.7±3.3	13.7±0.5	28

in northern Finland, and, the more so, for species of the genus *Formica*, with their deeply positioned nests. Two important circumstances should be emphasized: on the one hand, moderate (compared to cold-hardiness parameters of ants) lowest soil temperatures (even the absolute minimum values), and on the other hand, stable temperatures during the entire cold season due to early formed and thick snow cover: in December the average thickness of the snow cover in this area is as great as 41 cm, whereas in April it is 75 cm (Results…, 1979).

In the Northeast of Asia the overwintering conditions of ants are considerably more severe even in maritime areas. In the environs of Magadan the average temperature of January is −18.2 °C (average annual minimum −20.6 °C). The distribution of snow is extremely uneven, due to the strong and frequent winds. Temperatures in open snowless areas reach −32 to −36 °C at the surface of the soil and −26 to −29 °C at the depth of 20 cm (our unpublished data), and under 60 cm snow cover −17.0 and −5.3 °C, respectively (Berman et al., 1998).

A fundamentally different the situation, described in detail above, is formed in winter in the area of the Aborigen Field Station. In spite of the small distance from Magadan to Aborigen (around 2° of latitude or approximately 200 km), the climate of these areas is distinctly different. The strong warming effect of the sea is visible only in the narrow coastal strip proper, the width of which is hundreds of metres or a few kilometres, depending on the relief. The most striking result of this warming is the absence of permafrost or its presence of only in isolated pockets on the coast; outside the coastal strip, permafrost is continuous and influences all the components of ecosystems, including ants (Zhigulskaya & Berman, 1989). The influence of the sea gradually disappears towards the upper reaches of the Kolyma; in northeastern Yakutia it is negligible; and the meteorological stations Oymyakon, Moma, Delyankir and some others mark the area of highest continentality and the Pole of Cold of the Northern Hemisphere.

As noted above, in the upper reaches of the Kolyma the lowest temperatures at the surface of the soil (−25 to −43 °C) and at the depth of 20 cm (−21 to −33 °C) were recorded in localities with thin snow cover (0–20 cm), which generally occupy small areas. Snow cover of 20–40 cm, found in the overwhelmingly largest part of the area, preserves soil temperatures within the range −16 to −27 °C at the surface and −12 to −22 °C at the depth of 20 cm. Still thicker snow cover prevents soil temperatures from falling lower than −18 °C at the surface and −15 to −16 °C at 20 cm even at air temperatures close to −60 °C.

Cold-hardiness of ants in the environs Tvärminne, Kevo and Magadan. The most cold-hardy ant species of those studied so far is, as mentioned above, *L. muscorum* (Berman et al.,1982). In Oymyakon the lowest supercooling points recorded in this species reached −58.1 °C (larvae), while the average

supercooling point was −40.0±0.7 °C, ranging by around 4 °C, in adults (n = 166) from eight nests and −41.5±1.6 °C in larvae (n = 52) from two nests (Berman et al., 1982). In Tvärminne the supercooling points of *L. muscorum* from the studied nests were considerably higher than in these ants from the Northeast of Asia (Table 17). The lowest values recorded in ants from Tvärminne equalled the highest values in ants from the Northeast of Asia. The difference between the closest average values in ants from Tvärminne and the Northeast of Asia was around 8 °C (−23.9 to −31.6 °C) in larvae and almost 10 °C (−27.4 to −36.7 °C) in adults. In spite of the differences in supercooling point between ants from the Northeast of Asia and Tvärminne, the values of the depth of supercooling were relatively small and almost equal in adults (4.6 °C in Yakutia and 3.9 °C in Tvärminne) and different by 3 °C in larvae (1.1 and 4.2 °C, respectively).

The average supercooling point of *L. acervorum* from different nests at the Aborigen Station in winter (Table 18) vary within the range −36 to −43 °C in adults and −35 to −48 °C in larvae. Adults from nests of this species in the environs of Magadan, Kevo and Tvärminne display considerably higher average values of supercooling point, −22 to −27 °C; the lowest values of supercooling point in ants of these nests are also close to each other. Larvae have similar average values, but the low extreme is much lower (−27 to −37 °C), i.e. some of them even fall within the range of average supercooling points of larvae from nests at the Aborigen Station.

In *F. gagatoides* in the environs of the Aborigen Station average supercooling points from different nests vary from −27.5 to −30.3 °C; the average value of this parameter for 11 nests studied in winter is −28.6±0.2 °C (n = 467). Near Magadan and in Kevo the average supercooling points for nest were around −20 °C. The lowest values of the supercooling point of some individuals reached −35.3 °C at the Aborigen Station (Berman et al., 1987a) and −26 °C near Magadan and in Kevo, and everywhere they were only 5–6 °C lower than average values for the whole nest. All the above-discussed winter parameters for Magadan and Kevo and summer parameters for Aborigen, as Table 19 shows, constitute a series in which differences between values standing next to each other in the table are statistically insignificant (e.g. nests from Aborgien 6 June 1983 and Kevo 28 February 1992; Kevo 28 February 1992 and Magadan 16 April 1992), and only the winter values from the Aborigen Station are separated from the rest by a gap of 6 °C. The pattern of freezing points is almost the same, but the gap between the winter data from Aborigen and the rest of data is less than 3 °C, whereas the difference between the depth of supercooling of summer and winter ants is only 1.5...4.1 °C at the Aborigen Station and 2.7 °C in Kevo and Magadan.

F. lemani ants, in accordance with the greater protection of their overwintering chambers from low temperatures, at the Aborigen Station had supercooling points on the average 4–7 °C (see Table 19) higher and varying within a wider range than *F. gagatoides*. Average freezing points and the depth of supercooling of these two species were close to each other. Workers from different nests of *F. lemani* at the Aborigen Station in summer had average supercooling points from –13.5 to –19.1 °C and freezing points around –6 °C. In Kevo the cold-hardiness parameters of this species in winter were close to those at the Aborigen Station in summer, except freezing point, which fell in the range of winter values for Aborigen.

Among species of the genus *Formica* widely distributed in continental areas of the Northeast of Asia, *F. exsecta* is the least cold-hardy. In winter the average supercooling point in nests of this species from the Aborigen Station is –20.2±0.2 °C (n = 750); the depth of supercooling in ants from the studied nests showed little variance around 12–14 °C (n = 162), but reached 17 °C in some individuals (Berman et al., 1982), as in *F. gagatoides*. The average supercooling point of 46 individuals was around –16 °C in Kevo and only –10.7 °C in Tvärminne (see Table 19). However, extreme values of this parameter in Kevo and Tvärminne reached average values for nests at the Aborigen Station. The freezing points of ants from Kevo were identical to those of ants from the Aborigen Station, whereas the depth of supercooling in winter ants from the Aborigen Station was visibly greater than in ants from the other studied populations. Generally, as in the case of *F. gagatoides* and *F. lemani*, supercooling points in *F. exsecta* form a continuous series with a gap between Kevo and Aborigen.

*   *   *

The data on the cold-hardiness of ants from remote geographical populations presented above form a very clear picture if viewed together. In spite of considerable differences between autumn and winter temperature regimes of all the studied geographical localities, except the upper reaches of the Kolyma and the Indigirka, the results of our studies of different species show the same pattern. It is most fully displayed by the cold-hardiness parameters of *L. acervorum*, which were measured in all the studied localities (see Table 18; Fig. 58). In Tvärminne, Kevo and Magadan the winter cold-hardiness of every species is virtually identical, if not in total samples from different nests, then in intervals between pairs (lowest/highest) of average values from nests of each locality (see Fig. 59), while insects from the Aborigen Station have considerably lower values of cold-hardiness parameters.

Ants of the genus *Formica*, which belongs to a different subfamily (Formicinae) than *Leptothorax* (Myrmicinae), are on the average considerably less cold-hardy, but the distributions of cold-hardiness parameters in the studied
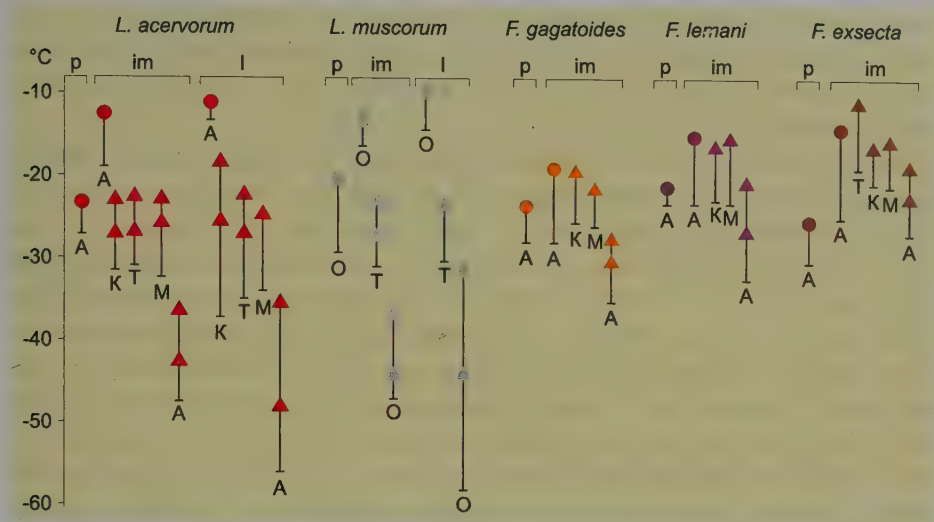
Fig. 59. Supercooling points (SCP) in different parts of the geographic ranges of some ant species. **A**, Aborigen, **K**, Kevo, **M**, Magadan, **O**, Oymyakon, **T**, Tvärminne. Circles, average supercooling point in samples of ants from particular nests in summer; triangles, in winter; p, pupae; im, imagines; l, larvae; line with crossing bar, lowest supercooling point value in the sample.

populations of different *Formica* species (see Table 19 and Fig. 59) display similar patterns to those found in *L. acervorum*. Results shown in Fig. 59 suggest that the data on *L. muscorum*, the cold-hardiness parameters of which were measured only in Tvärminne and Oymyakon, represent are fraction of a picture similar to that of *L. acervorum*.

Cold-hardiness and climatic conditions. The climate differences of the studied areas are close to the greatest possible in Eurasia at latitudes 60–70° in winter. Within the ranges of the species found in the warmest of the studied localities, Tvärminne, still warmer areas may be found in southeastern Scandinavia. All the data presented above suggest that the winter cold-hardiness of the discussed ant species would be no less in these areas than in Tvärminne. By contrast, ants from northeastern Yakutia (*L. muscorum*) and from the Aborigen Station (the other species) probably display the greatest cold-hardiness they can currently have. As noted in the previous section, ants at the Aborigen Station already by mid-October reach levels of cold-hardiness found in ants of Tvärminne, Kevo and Magadan in February. In late October the cold-hardiness, for instance, of *L. acervorum* larvae at the Aborigen Station can reach record values for this species: average supercooling point in a nest –48.2±2.3 °C. From this point and

until late April ants of all the species studied at the Aborigen Station are exposed to negative temperatures and, judging by the results of awaking ants from nests excavated in winter and by the values of $LT_{50\%}$, survive these temperatures quite successfully.

Fig. 59 and comparison of Tables 17, 18 and 19 show that in all the studied localities, except the Aborigen Station, we probably deal with insects employing only a small fraction of their physiological capacities in addition to their summer non-specific cold-hardiness. This small fraction proves to be sufficient for their successful overwintering in areas with relatively mild temperature regime under the snow cover, either because of sufficiently high air temperatures or because of the thickness of the snow. In the second half of winter and in spring ants, as well as some other insects (Ushatinskaya, 1987), evidently remain in the state of chilled coma: after warming (even rapid) they start running, making work with them quite difficult for the experimenter. It should be emphasized that in this case the cold-hardiness of insects is a "side effect" of the state of diapause, and not a specific adaptation. Thus, it is natural to suppose that vast areas of northern Eurasia with stable snow cover, except the ultracontinental parts, could have been colonized by ants through to this preadaptaion to winter cold.

The phenomenon of the great cold-hardiness displayed by ants in the cold continental areas of the upper reaches of the Kolyma and the Indigirka doubtlessly reflects the peculiar climate of these areas. The autumn temperature regime is probably crucial for the formation of this winter cold-hardiness. Unfortunately, we cannot name with certainty the particular factor conductive to extreme cold-hardiness: either the huge daily range of air temperatures (−15 to +15 °C) in late September, or abrupt falls of soil temperatures in the absence of snow cover or under thin snow in October and November, or the more smooth, but long decrease of temperatures in the first half of winter. In the other studied areas autumn is considerably milder, either because of early and rich snowfalls or because of higher air temperatures.

Revealing the process responsible for the cold-hardiness of ants from the environs of the Aborigen Station requires thorough special studies; this process may prove to be a combination of diapause and acclimatisation. Because of the above-mentioned huge daily range of air temperatures in late September, acclimatisation may include such reactions as rapid cold hardening or even cold shock. As explained at the beginning of this chapter, acclimation is understood as the influence (both process and effect) of gradually decreasing temperatures in laboratory experiments, usually in the course of days or weeks, whereas acclimatisation is understood as the same process and effect, but at gradually decreasing seasonal temperatures in nature (Block, 1995); cold shock is abrupt decrease of temperature to values close to zero for minutes or hours (Sinclair &

Roberts, 2005). These notions and corresponding processes are at present reconsidered and intensely studied (Bale, 2002; Sinclair & Roberts, 2005), mostly on well-known model organisms, such as fruit flies.

Only in the coldest areas, such as the upper reaches of the Kolyma and the Indigirka (and probably also in the upper reaches of the Yana, in central Yakutia and in other areas with very cold winter) considerable amounts of cryoprotectants of diverse nature are accumulated in *Formica* and *Leptothorax* under the direct influence of negative temperatures (Leirikh, 1989).

The synthesis of glycerol was observed at temperatures lower than 5 °C, continuing at least until temperatures as low as –17 °C (Ring & Tesar, 1980). The dependence of the activity of enzymes responsible for polyol synthesis on the physiological state of the organism was studied in recent years in a number of insect species. It was found that the synthesis starts under the influence of temperatures lower than 5°C, but only in insects already diapausing, and is effective at early, but not at late stages of diapause (Kostal et al., 2004a, 2004b). The physiological state of ants in cold continental climates is probably most favourable for the accumulation of cryoprotectants by the moment of the autumn fall of soil temperatures. Figs. 46, 47 show that the synthesis of polyols in the course of seasonal acclimatisation in the ants *L. acervorum* and *C. herculeanus* at the Aborigen Station starts in September, but by the end of October only 50% of their largest amount, recorded in January–February, is accumulated. Different proportions of parameters determined by diapause and acclimatisation can probably have quite different combined effect; this is confirmed both by results of our studies of ants from different genera and by examples found in the literature. For instance, the cold-hardiness of diapausing insects can be quite considerable even at relatively high above-zero temperatures of the environment. According to Merivee (1971a), supercooling points of a number of insect species after the start of diapause reached extreme values in animals kept in the laboratory at 20° much sooner than in control animals in their natural environments; the supercooling capacity of almost all the studied species at 20° had values close to the highest, observed in these species in winter at the period of their greatest cold-hardiness.

The course of acclimatisation, in its turn, can differ, as all the other cold-hardiness-related processes, in members of different insect groups and sometimes even in different species of the same genus: in some insects the rate of acclimatisation is directly dependent on temperature and humidity (Sheldeshova, 1972), while in others acclimatisation takes 1.5 months even under optimal conditions, and the effect of the temperature of the environment –13°C is relatively small in comparison with the effect of –6°C (Merivee, 1971a). Since neither acclimatisation and diapause of the ant species found at the Upper Kolyma nor the winter content of cryoprotectants in all the populations except those from

the Aborigen Station were specially studied, it remains unclear, whether ants dwelling in areas with relatively mild winter are capable, like the populations of ultracontinental areas, of considerably increasing their cold-hardiness under the optimal regime of acclimatisation. Judging by the lowest values of cold-hardiness parameters recorded in ants from Tvärminne, Kevo and Magadan, this process is principally possible.

As shown in the section of this chapter on the dependence of cold-hardiness on microclimate, the difference in lowest temperatures −12 to −14°C and −20 to −25°C between areas with nests of with *L. acervorum* results in only 2°C difference in cold-hardiness. Thus, acclimatisation is either completed at higher temperatures (higher than −12°C), or determined by other climatic parameters, e.g. duration of exposure to temperature below some threshold value in autumn, daily range of temperature, etc. Most probably, a suitable combination of diapause end exposure to negative temperatures predetermine the usage of reserve substances for synthesis of cryoprotectants, rather than for supporting the vital functions of ants that completed their diapause at low positive temperatures, which is possible if the autumn is mild and the winter not very cold.

Finally, we would like to draw attention to a fact we revealed but have not explored, giving some hope that predictions of cold-hardiness parameters are achievable without carrying out extremely labour-consuming winter studies in nature. The foundations for such predictions are clearly demonstrated in Fig. 59, where data on summer (July–August) cold-hardiness of the pupae of the studied insects are presented. Pupae of species of the genus *Formica*, as well as other juvenile stages of development in ants of this genus, never overwinter, and their cold-hardiness has no adaptive value. And yet the cold-hardiness of *F. exsecta* pupae is greater than that of overwintering adults in all the studied areas, including, what is especially important, even the environs of the Aborigen Station. Pupae of *F. gagatoides* and *F. lemani* are less cold-hardy than pupae of *F. exsecta*,

Table 20. Cold-hardiness (°C) of pupae of the genus *Leptothorax*

Species	Supercooling point			Colouration of pupae
	m ± SE	min	n	
L. acervorum (Aborigen, 26.VII.1978)	−23.3 ±0.4	−27.0	28	Light
	−16.0 ±0.9	−26.2	19	Dark
	−20.3 ±3.3	−27.9	15	Light
L. muscorum (Oymyakon, 9.VII.1979)	−13.0 ±2.2	−27.3	15	Dark
	−19.2 ±3.0	−27.6	16	Light
	−15.2 ±2.5	−25.6	16	Dark

Note. In brackets, locality and date of measuring.

so this character is not generic. The situation with pupae of both *Leptothorax* species is more complicated, since pupae of different stages of development may be present in nests of these species in summer. Extreme cases are easily distinguished both by habitus (colouration) and by cold-hardiness (Table 20). Light pupae at the beginning of their development have greatest cold-hardiness; dark pupae are completing their development, and their cold-hardiness is close to that of emerging adult ants.

SOME GENERAL RESULTS

To sum up all the findings presented in this chapter, let us note some general points. The values of cold-hardiness parameters of all the nine ant species studied in a single geographical locality form practically continuous series of average supercooling points from −19 to −40 °C and of $LT_{50\%}$ from −12 to −35 °C. The most rapid changes in the supercooling point of all the species are observed in autumn (September–October), but later cold-hardiness continues to increase, during the entire period of negative temperatures, more considerably in November–December, and probably slowly growing until the melting of snow. In other words, values of supercooling points close to lowest hold for 5 months (from December to late April).

Increase of cold-hardiness is accompanied by synthesis of low-molecular antifreezes, namely sugars and polyols. Low average supercooling points are provided by the accumulation of quite considerable amounts of polyols (up to 16% in workers and 24% in larvae of *L. acervorum*, *L. muscorum* and *C. herculeanus*), close to record amounts known in wintering insects (Hansen, 1980a, 1980b; Ring & Tesar, 1981).

Mortality at low sub-zero temperatures in ants, as in a number of other insect species studied earlier, is linearly dependent on the logarithm of exposure duration. Therefore mortality at 24-hour exposure to constant low temperatures is a sufficiently representative measure of the reaction of ants to possible natural conditions. Temperature lethal to a half of the individuals after 24-hour exposure ($LT_{50\%}$) was chosen as a measure of the tolerance of ants to long-term exposure to low temperatures. This parameter is similar to the one used in studies of freeze-tolerant invertebrates.

Since we used very large samples in our study, a very informative parameter was the difference between average supercooling point and lowest long-term tolerable temperature. This parameter not only allows comparing species with each other, but also vividly represents seasonal changes. In winter the lowest long-term tolerable temperature is higher than average values of the supercool-

ing point by 1.5–3.5 °C in *F. gagatoides*, by 2.5–4.5 °C in *M. kamtschatica* and *M. bicolor*, by 5 °C in *L. acervorum* and *F. sanguinea*, and by 6–7 °C in *F. lemani* and *F. exsecta*; *F. gagatoides* and *F. lemani* are capable of surviving deepest super-cooling (by up to 13 °C), while all the other species can survive supercooling by at most 4–5 °C. In summer the differences between supercooling point and lowest long-term tolerable temperature in members of the genus *Formica* are on the average somewhat greater, 7–9 °C, so that they are able to survive in experiments at temperatures as low as –8 °C. This considerable summer resistance to low sub-zero temperatures should be viewed, apparently, as non-specific. Such resistance is deemed generally uncharacteristic of insects of middle latitudes (Lee & Denlinger, 1991), though in our opinion there is not enough foundation for this assertion, since the phenomenon has been poorly studied.

Since in summer $LT_{50\%}$ is equal to freezing point or higher (in winter it is always lower), the main indicator of the seasonal increase in cold-hardiness of this group of species, in addition to the decreasing supercooling points, is the stabilisation of the supercooled state. In summer, decreases of body temperature below the freezing point of bodily fluids (apparently accompanied by the stochastic process of formation and destruction of ice nucleators) very soon result in freezing, whereas in winter the growth of forming ice nucleators is suppressed by certain agents, which we have not determined, probably by antifreeze polypeptides, and the supercooled state is maintained for months. In species least resistant to cold in winter (*F. exsecta*, *F. sanguinea* and *F. lemani*) the value of the lowest long-term tolerable temperature changes from summer to winter only by 3–6 °C.

CHAPTER 5
ON THE CONNECTION OF COLD-HARDINESS, OVERWINTERING TEMPERATURE CONDITIONS AND SPATIAL DISTRIBUTION OF ANTS

Data on the habitat distribution of ants, the ecology of their overwintering and their resistance to cold, presented in previous chapters, allows determination of whether the spatial distribution of these insects is limited by the temperature conditions of their overwintering.

All the studied ant species can be divided into three groups on the basis of their resistance to cold. The most resistant species are *Leptothorax acervorum*, *L. muscorum* and *Camponotus herculeanus*: their supercooling points are around –40 °C. *F. gagatoides* and both *Myrmica* species are considerably less resistant: their supercooling points are from –27 to –31 °C. The other species of the genus *Formica* have little cold-hardiness: their supercooling points fall in the range –18 to –25 °C (Table 21).

GROUP I (*L. acervorum, L. muscorum, C. herculeanus*)

Among all the ants of the Northeast of Asia, *L. acervorum* occupies the widest range of habitats and has in this area the highest abundance of all known from the literature and from our studies. The well-being of this species is largely determined by its very extreme cold-hardiness. The average value of the supercooling points of wintering adults and larvae is –40±0.2 °C. Judging by the values of supercooling points and the results of experiments on the survival of *L. acervorum* at low negative temperatures, we can be sure that 50% mortality after long-term exposure is observed at temperatures below –32 °C, but even at –40 °C some of the ants survive. The distribution of the supercooling points of workers in every nest is very compact: variation coefficient is usually relatively low, 8–15%. The highest supercooling points recorded in adults are no higher than –35 °C, while the lowest are –44 to –45 °C. Nests with deviations from the

Table 21. Overwintering conditions and cold-hardiness of abundant ant species in the Upper Kolyma area

Species	Habitat distribution	Depth of over-wintering chamber position, cm	Overwintering conditions, °C			Cold-hardiness parameters, °C			Cryoprotectants, % wet mass
			Average lowest temperatures in most of the Kolyma area at the depth of wintering	Normal seasonal lowest in nests	Lowest recorded temperatures in wintering chambers	Super-cooling point	Lowest long-term tolerable temperature (50% mortality)	Reserve	
L. acervorum	Almost everywhere in sparse forest belt	2–7	–24 to –27	–24 to –27	–30	–38 to –43	–32 to –35	10	15–20% (glycerol)
L. muscorum	Very locally	7–10	–24 to –27	No data	–25	–37 to –44	No data	?10	30–40% (unidentified polyols)
C. herculeanus	Almost everywhere in sparse forest belt	0–10	–24 to –27	–14 to –25	–30	–37 to –40	–28 to –34	10	15–20% (glycerol)
F. gagatoides	the same	10–25	–16 to –24	–16 to –22	–25	–27 to –30	–24 to –28	4–6	up to 5% (sugars + polyols)
M. kamtschatica	Locally	10–25	–16 to –24	–16 to –18	–28	–27 to –31	–23 to –28	5–7	10% (unidentified polyols)

M. bicolor	the same	30–40	–18 to –22	No data	–20	–27 to –31	–23 to –26	4–6	10% (unidentified polyols)
F. candida	the same	25–50	–15 to –22	No data	–20	–24 to –25	–18 to –19	0–2	6% (sugars)
F. exsecta	Spotted	10–130	–6 to –24	–10 to –13	–13	–19 to –22	–12 to –15	2–3	2% (sugars)
F. sanguinea	Locally	20–40	–18 to –24	–10 to –13	–13	–17 to –18	–12 to –14	2–3	3% (sugars)
F. lemani	the same	60–140	–6 to –12	–10 to –15	–12	–20 to –24	–15 to –17	2–5	5% (sugars)

mentioned average values greater than 1 °C are relatively rare: only in three of the 22 nests examined in winter the supercooling points of workers were around −37 to −38 °C (from −30 to −41 °C), and in one nest they reached−42.2 °C (from −38 to −46 °C). The number of workers insufficiently prepared for winter in each nest is very low: in a nest with 50–60 individuals, only 1–2 ants have abnormally high supercooling points (around −20 to −25 °C). Successful preparation for overwintering is also demonstrated by the high proportion of worker ants awakening in winter in laboratory conditions (95–100%). The temperature parameters of overwintering larvae vary within a wider range: in samples of the same size as those of workers, variation coefficient is more than twice as high, 33–37%. However, even among larvae the proportion of individuals with very low (below −45 °C) supercooling points is high.

This resistance to low temperatures allows *L. acervorum* to overwinter at depths of only 5–7 cm virtually in all the Upper Kolyma area, except snowless spots on plateau-like surfaces and the upper parts of slopes (see Table 9, nos. 1, 2). Cold-hardiness plays an important part in providing the success of this species, giving it the opportunity to use the advantages of dwelling at the surface of the soil. The position of its overwintering chambers close to the surface helps ants of this species to awake early in spring, prolong the period with positive temperatures by 1–2 weeks, compared to the nests of *M. kamtschatica* and *F. gagatoides*, and to 1 month, compared to the nests of *F. exsecta*.

Some limits on the microhabitat distribution of this species can probably be imposed by the patchy character of snow cover and the related heterogeneity of temperature field. The temperatures we recorded in some areas of mountain tundras and the sparse forest belt were close to the lowest tolerated by this species: in frost polygons and areas with thin snow cover in dwarf-shrub–lichen tundras (see Table 9, nos. 3, 7, 8), on a snowless steppe slope (no. 4), as well as on trains of slopes, but only at the tops of moss tussocks (nos. 22, 23). However, the absence of *L. acervorum* in the mountain tundra of northern, west- and east-facing slopes and the low abundance of this species on dry south-facing slopes are by no means caused by the limiting effect of low winter temperatures.

The closely related *L. muscorum* has exactly the same supercooling points as *L. acervorum*. The proportion of individuals dying in winter is also small, 5%. Taking into account the similarity of mechanisms responsible for cold-hardiness, we may assume that 50% mortality after long-term exposure will be observed, as in *L. acervorum*, at temperatures 4–5 °C higher than average supercooling points, i.e. −32…−39 °C.

The only habitat of *L. muscorum* in the Northeast of Asia, steppe areas of slopes, is among the coldest habitats of the region in winter, because of the dry substrate, deep position of the permafrost surface and small thickness of the

snow cover. Nevertheless, the difference between the supercooling point and lowest temperature in the nest reaches 16–18 °C, which allows ants to survive even more severe conditions, which can form in the soil as a result of either falls of air temperature or the thinning of the snow cover by winds. The lowest of the values of supercooling point found in larvae (−58.1 °C) is comparable to the lowest air temperature we recorded (−59.8 °C). Even at still lower air temperatures, as low as −69 °C (Spravochnik…, 1966), the soil of the horizon 5–15 cm deep under the cover of snow 20–30 cm thick, can be cooled to temperatures no lower than −40 °C (Pavlov, 1979). The lowest supercooling point of adults is close to −50 °C, and the proportion of ants with supercooling point lower than −45 °C is around 11% of all the studied individuals from 10 nests. Moreover, we cannot exclude the possibility that still lower supercooling points can be found in *L. muscorum* by examining large samples of ants from a greater number of nests. Apparently, some individuals survive even under the most unfavourable wintering conditions. Thus, extreme cold-hardiness allows *L. muscorum* to hold its ground in these coldest areas. All this clearly shows that the distribution of this species in the Northeast of Asia is not in the least limited by overwintering conditions, but is determined exclusively by summer conditions.

L. muscorum, like *L. acervorum*, enjoys the above-described advantages of the surface nest position. But unlike *L. acervorum*, *L. muscorum* can exist at extremely low soil water content; such soils evaporate little and are, thus, very strongly heated. No other ant species of our fauna can build its nests in such conditions.

Xerophyte slope areas of the upper reaches of the Kolyma and the Indigirka have a similar duration of the warm season and similar highest values of soil temperatures. The main difference limiting the distribution of *L. muscorum* is probably related to continentality of climate. Cyclones from the coast of the Sea of Okhotsk bring cloudy weather with winds and rains to the Upper Kolyma more often than to the Indigirka, making the soils of the Kolyma more humid and somewhat more often cooled to temperatures equal to those in the air. There are, however, no reasons to think that *L. muscorum* is unable to prolong its development by 2–3 years in cases of heat deficiency, in the same way that *L. acervorum* does. Thus, the most likely reason for the absence of *L. muscorum* in the Kolyma basin is historical. The area occupied by relict steppes in the upper reaches of the Kolyma is small, compared to that of the Indigirka. This alone makes the probability of long preservation of relict species much lower in the Kolyma valley than in the Indigirka valley: a population that once for any reason died out in an isolated area can be restored with probability inversely proportional to the distance from the nearest area with preserved population of this species.

C. herculeanus is the third species of the most cold-hardy group. Average supercooling points of overwintering adults and larvae of *C. herculeanus* are 2–3 °C higher than in the two other species (see Table 21). In addition, nests of *C. herculeanus* usually include more dead ants (up to 20% in some chambers) and ants insufficiently prepared for overwintering, whose tissues freeze simultaneously with crop content at −12 to −26 °C (their proportion is as great as 30% in some chambers). The proportion of individuals awaking in winter in laboratory conditions varies from chamber to chamber also quite considerably (from 60 to 90%). However, in general (in all the examined nests taken together) almost half of the individuals can be supercooled to temperatures below −40 °C, and around 11%, below −45 °C, which shows resistance to low temperatures no weaker than in the two other species of this species group.

We believe that the presence of groups of individuals with different cold-hardiness parameters in nests of *C. herculeanus* does not imply that the conditions of the Northeast of Asia are unfavourable to this species. This heterogeneity is probably related to the considerable complexity of the social organization of *C. herculeanus*, compared to that of the two other species of this species group, and, consequently, with some differences in the physiology and biochemistry of some groups of individuals. It is also possible that individuals insufficiently prepared for wintering constitute a part of the nest's population that naturally dies off in winter. The final verdict will be pronounced only after comparing the data on the winter mortality in nests of this species in the Northeast of Asia with similar data from parts of its range with milder winters.

The capacity of this species to survive long-term exposure to low temperatures was not studied. However, taking into account the similarity of the mechanisms providing cold-hardiness in *C. herculeanus* and *L. acervorum*, we may suppose that 50% mortality of individuals of this species will be observed also under temperatures 5 °C higher than the average supercooling point, i.e. −31 to −35 °C. And if we take into account the extremely heterogeneous composition of the population of different nests and the greater average proportion of individuals poorly prepared for wintering, we should conclude that the values of $LT_{50\%}$ in *C. herculeanus* are probably still higher. It is probably best to consider 30 °C as the temperature limiting the distribution of this species.

Thus, the same infrequent snowless rubbly areas are unsuitable also to *C. herculeanus* because of their temperature conditions during the cold season. Because of body and nest size, considerably greater than in *L. acervorum*, the habitat distribution of *C. herculeanus* is determined by factors other than lowest temperatures. The most important of these factors is the availability of sufficient localities for nest-building. *C. herculeanus* builds its nests in stumps and fallen tree trunks with solid wet wood, in the destruction of which it plays a key part.

The heat supply of habitats is probably of secondary importance, since the mosaic character of conditions invariably provides a suitable place for warming the brood close to the nest, whether under a piece of bark or under a flat stone.

Apparently, this group of species is capable of living everywhere, except in the rare snowless biotopes. However, in fact only *L. acervorum* and *C. herculeanus* are found everywhere. The strict confinement of *L. muscorum* in the Indigirka valley to steppe areas probably reflects some factors of summer conditions; the most obvious suggestion would be heat supply, many times greater in steppes than in surrounding biotopes. However, the presence of this species in pine forests near Okhotsk (see Chapter 2) indicates the role of other factors, probably reflecting biotic relationships. As for the absence of *L. muscorum* in the Kolyma basin, it most probably reflects, as noted above, the history of the area.

GROUP II (*F. gagatoides, M. kamtschatica, M. bicolor*)

Species of this group are considerably less cold-hardy; in winter their average supercooling points fall are −27 to −31 °C (see Table 21). Homogeneity of the cold-hardiness parameters of individuals within each nest is characteristic of all the three species: the highest values of supercooling point are never higher than −24 to −25 °C, while the lowest reach −34 to −35 °C, and variation coefficient is 6 to 14%. The proportion of individuals dying during winter is usually as low as 4–6%. Lowest long-term tolerable temperatures fall within the range −23 to −26 °C in both *Myrmica* species and −24 to −28 °C in *F. gagatoides*.

Greater, compared to the first group, stability of the supercooled state is of crucial importance to this group, since its freezing points are relatively high: only −16 to −20 °C in workers of *M. kamtschatica* and −12 to −13 °C in *F. gagatoides*, while the temperatures we measured in their nests reached −16 to −18 °C, and in some years even −25 °C. In other words, individuals remained in the supercooled state in periods of lowest temperatures for several days in *M. kamtschatica* and for up to a month and a half in *F. gagatoides*.

Temperatures from −23 to −27 °C should be considered limiting for the distribution of this group of species. Such values of the lowest seasonal temperatures were recorded at the depth of 15–20 cm in rubbly snowless areas of the sparse forest belt and in most examined areas of the mountain tundra (except leeward parts of south-facing slopes with thick snow cover). Thus, the amount of plots unsuitable for colonization because of temperature conditions is not much greater in this group of species than in the first group. Therefore, factors other than lowest soil temperatures are limiting the distribution of *F. gagatoides*, *M. kamtschatica* and *M. bicolor* and have to be determined.

The most important factor limiting the habitat distribution of *F. gagatoides* is the high level of underground water (30–40 cm). As for the low abundance of this species on dry south-facing slopes, it is probably caused by the extreme dryness of the upper soil horizons it inhabits and its conservative nest-building, due to which ants of this species never reach deeper than 30 cm into the soil, even in deeply thawing areas.

The exclusively local habitat distribution of *M. kamtschatica* is determined by a combination of heat and humidity. The sum of temperatures at the surface of a moss tussock is somewhat smaller than in the upper layer of the soil on dry south-facing slopes (their advantage mainly provided by the longer warm season due to the early melting snow cover), while the humidity regimes of these two microhabitats are incomparable. Thus, *M. kamtschatica* has a preference for the warmest of humid microhabitats.

The reasons for the preference of *M. bicolor* for floodplain pebbly areas with young growth of poplar and chosenia remain unclear. This preference is probably also unrelated to temperature conditions of the cold season, since temperatures from –15 to –20 °C at depths greater than 20–30 cm are characteristic of most areas of the sparse forest belt.

GROUP III (*F. candida, F. exsecta, F. sanguinea, F. lemani*)

Unlike the other two groups, which include members of different genera with quite close values of cold-hardiness parameters, this group is constituted of three of the four species of the genus *Formica* dwelling in the Upper Kolyma area. Species of this group differ in the degree to which their resistance to cold differs from that of the previous group, and their habitat distribution is spotted.

The member of this group most sensitive to cold is *F. exsecta*: average supercooling points of ants in different nests are from –19 to –22 °C (see Table 21), with variation coefficient 12–22%. *F. sanguinea* has a similar degree of sensitivity to cold; unfortunately, only one nest of this species was examined; the supercooling point of ants from this nest was –17.2±0.5 °C (n = 46). The supercooling points of two other species are slightly lower than in *F. exsecta*: the range between average values for ants of different nests was from –20.7±0.5 to –23.1±0.6 °C in *F. lemani* and from –24.2 to –25 °C in *F. candida*.

As in the two other groups, 50% mortality after 1–3 days of exposure is observed at temperatures higher than average supercooling points by 5–6 °C in *F. exsecta* and *F. sanguinea*, and by 7 °C in *F. lemani*. Thus, the temperatures limiting the distribution are around –12 to –15 °C in *F. exsecta*, –12 to –14 °C in *F. sanguinea*, –15 to –17 °C in *F. lemani*, and around –18 to –19 °C in *F. candida*.

Let us discuss in more detail the habitat distribution of *F. exsecta*, the species most dependent on winter conditions in particular. Comparison of these conditions, which appeared to be almost identical in nests from different areas, with cold-hardiness parameters, at first glance seems to imply the presence of a considerable physiological reserve, as the temperatures observed in nests appear to be very far from the lowest long-term tolerable values. Indeed, in most cases the lowest temperatures in the nests are 8–12 °C higher than supercooling points and only 1–3 °C lower than freezing points. In other words, no more than a quarter of the supercooling capacity (at least 13 °C) is realized in these ants.

Meanwhile, the pattern of habitat distribution leaves no doubt that the existence of *F. exsecta* in all the studied areas, except the depression of Jack London Lake (see below), is unstable. This instability is reflected in the rare occurrence not only of nest groups, but also of separate nests, in the small size of the groups themselves, the small size of cones, and especially in considerable numbers of dead nests, in many areas many times greater than the number of living nests.

The causes of such distribution are most probably diverse, but the most likely determinants are the following two complementary factors:

1. The observed—residual—pattern results from an unfavourable climatic fluctuation in one of the past winters, namely, a combination of small snow cover density with low values of lowest air temperatures, which resulted in a fall of soil temperatures intolerable to ants of this species.

2. *F. exsecta* in the studied habitats of the area, except the depression of Jack London Lake, constantly exists at the limit of its physiological capacity. Approximate calculations show that in winters longer than 7 months the duration of exposure to temperatures below −5 °C in overwintering chambers of this species is over 4 months, and to temperatures from −8 to −10 °C, almost 2 months. Thus, ants remain in the supercooled state for more than a quarter of their overwintering period. Moreover, the supercooling points of a small proportion of individuals are even higher than lowest overwintering temperatures, making the death of these individuals in winter inevitable. The proportion of ants dying in the course of overwintering is a quantitative measure of the combined effect of long-endured supercooled state and insufficient cold-hardiness of some individuals. In experiments with *F. exsecta* awaking in laboratory conditions, the proportion of dead individuals was 8–30%. As noted above, in *F. gagatoides*, *L. acervorum* and *M. kamtschatica* as many as 94–96% of individuals successfully awake in such conditions. The final verdict on the tolerance of ants of this species to cooling of different degree and duration can be reached only after special comparative studies on the proportion of ants dying at different temperature regimes, as well as of the natural mortality in the course of overwintering in the Northeast of Asia and in other parts of the range.

Indirect evidence of the proximity of temperatures observed in nests to the lowest tolerable temperatures is given by the absence of *F. exsecta* in all localities where the lowest temperatures are below −13 °C at the depth where overwintering chambers of this species can be positioned. This conclusion is based on the analysis of temperature courses in over 40 localities from all the principal habitats of the altitudinal zonal profile characteristic of the Upper Kolyma basin, differing in altitude, exposure, humidification etc. All this suggests that the overwintering of *F. exsecta* can be successful only at differences between the temperature in overwintering chambers and the average supercooling point of at least 5–7 °C; a decrease of the lowest temperature in the nest by only 1 °C proves lethal to the overwintering ants.

In the depression of Jack London Lake a thick cover of loose snow, forming 2–3 weeks earlier than in valleys, and winter air temperatures slightly higher (by 5–7 °C), due to greater true altitude, probably always provide both more favourable soil temperatures near the surface and greater homogeneity of the temperature field. Temperatures at the level of soil surface under the domes of nests in this depression differ at most by 1.5 °C (distance between nests over 200 m), whereas in a larch forest on a terrace of the Olen Brook differences between such temperatures reach 4.5 °C (distance between nests around 50 m).

Evidence of the favourable conditions enjoyed by *F. exsecta* in the depression of Jack London Lake is provided by the mushroom shape of its nests found in this depression, but not anywhere else in the study area. The overwintering chambers of these nests are positioned at the level of tussock bases, and therefore the temperature regime in these chambers is determined (apart from air temperatures) virtually exclusively by parameters of snow cover. Mushroom shape, in combination with the density of nests, very high for our study area, is undoubtedly evidence of stable conditions favourable to *F. exsecta* maintained over long periods of time. Thus, the impression is that the habitat distribution of this species in the study area is largely controlled by overwintering conditions. Because of its limited cold-hardiness, *F. exsecta* is capable of colonizing only special localities, with the upper horizons of the soil particularly warm in winter. In summer these areas should be moderately humid, in many cases due to the small depth (50–60 cm) of the seasonally thawed layer.

The well-being of *F. exsecta* in areas of greater altitude may be viewed as an altitudinal shift of the optimum, following the increase of winter air temperatures and thickness of the snow cover, but in spite of summer conditions getting less favourable with altitude: shorter snowless period (by 10–20 days) and vegetation period (by 10–15 days) and lower average monthly temperatures (by 1–1.5 °C in July). A similar shift from valleys to higher mountain areas with altitudes 1600–2200 m above sea level was described in *F. exsecta* in the Balkans

(Atanassov, 1952), where the cause of this shift is apparently the opposite: summer temperatures in the valleys too high for this boreal mesophile species.

The revealed peculiar character of the habitat distribution of *F. exsecta* explains why this species is absent in the Oymyakon depression, or rather within the part of its bottom examined by census routes. In the Upper Kolyma region, overwintering conditions determine the position of nests only in special localities; in the Oymyakon depression, due to lower air temperatures and smaller thickness of snow cover, such localities probably occur at the same altitudes less frequently, and we failed to find them. The above-described preference of *F. exsecta* for the belt 600–1000 m above sea level suggests that in northeastern Yakutia this species can also be found in similar conditions, but probably somewhat higher (at 800–1200 m).

The summer temperature requirements of *F. exsecta* are apparently also rather strict, judging by the absence of this species in biotopes with winter conditions quite suitable for its existence. The limiting effect of summer conditions on the distribution of *F. exsecta* is reflected in its avoidance of shaded areas: in sufficiently illuminated localities, piled-up cones help ants to accumulate considerable sums of above-zero temperatures, comparable with those accumulated on south-facing sides of moss tussocks or mountain slopes. This species is also absent from south-facing slopes excessively dried from the surface to the depth of 20–30 cm, even if the conditions of such slopes are satisfactory for overwintering at depths of 1–1.5 m. It should be noted that *F. exsecta* displays highest plasticity in nest organization, which allows colonizing even tussocks of sedge waterlogged areas, where other species of ants are absent[1].

We have not much to say on the habitat distribution of *F. sanguinea*, since this species is rare everywhere in the study area, and the data at our disposal are insufficient for analysis. Judging by the available data, we may suppose that in the Northeast of Asia *F. sanguinea* is limited in its distribution by winter temperatures to the same extent as *F. exsecta*, but its requirements of summer condi-

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[1] Reconnaissance surveys of the density of *F. exsecta* nests were carried out again along the landscape profile of the Aborigen Station in 2004 (Goryunov, 2005; Alfimov, personal communication). It was found that 25 years after the end of regular studies this species had become considerably more widespread in the mountain forest belt. Thus, the picture described above most probably resulted from a climatic fluctuation (lack of snow at very low air temperatures), which took place no later than the late 1960s or early 1970s and ruined most of the *F. exsecta* population in this area, which subsequently recovered during the last few decades. Analysis of long-term trends of air and soil temperatures and thickness of the snow cover, based on data of the Hydrometeorological Service, is planned to test this hypothesis.

tions are probably stricter. *F. sanguinea* is found only in a small proportion of the biotopes inhabited by *F. exsecta*; it avoids both overwetting areas and upper parts of the sparse forest belt, possibly because of unsuitable heating conditions. It is remarkable in this connection that we have not found this species in the depression of Jack London Lake while we studied *F. exsecta* colonies of this depression.

F. lemani, another species of this group, has the same degree of resistance to cold as *F. exsecta*. However, its method of choosing sites for nest-building is different: *F. lemani* avoids low temperatures, overwintering at depths of 60 to 140 cm. Therefore, in continental areas this species preferably colonizes deeply thawing (over 2 m) dry south-facing slopes; extreme dryness of the ground makes them close to steppe soils. This preference for dry south-facing slopes is virtually absent in *F. lemani* at the coast of the Sea of Okhotsk, where winter temperatures are considerably higher, and where *F. lemani* has incomparably wider distribution, including the mesophyte series of biotopes.

The most cold-hardy species of this group is *F. candida*, which occurs in several types of habitats: floodplain pebbly areas (where it is an abundant species), steppe areas (where it was found only on a single slope) and on a waterlogged train (also a single case). Large colonies of this species are characteristic of pebbly areas in floodplains of large rivers; wintering chambers are positioned in such areas at the depth of 40–60 cm. In coldest winters, when the riverbed partly freezes, temperatures in the nests may reach values close to the lowest tolerable.

Required winter temperatures in steppe areas are provided by building nests in erosional depressions, always covered with snow; in moss tussocks on a train of a south-facing slope this species probably exists at the limit of its physiological capacity, which is, as noted above, greater than in any other species of the third group.

The habitat distribution of *F. candida* in the Northeast of Asia shows, on the one hand, that this species remains faithful to at least some of the biotopes it prefers in South Siberia (Zhigulskaya, 1968), provided that their hydrothermal regime allows building wintering chambers deeper than 30 cm and avoiding temperatures lower than −18 to −20 °C. On the other hand, the fact that there are only two findings of *F. candida* nests on steppe slopes and very few nests were found in only one of the many examined waterlogged mossy slope trains suggests that in this case, as in the case of *F. exsecta*, the population recently collapsed, following a thermal catastrophe in the recent past.

Thus, three groups of ant species are recognised on the basis of the degree of limitations imposed by overwintering conditions on their spatial distribution. The most cold-hardy, *L. acervorum*, *L. muscorum* and *C. herculeanus*, are virtually not limited in their habitat distribution either in the mountain forest belt or in the mountain tundra belt. In all the study area (except in the rare snowless spots) the

difference between the lowest temperatures in the soil at the depth of 5–7 cm, where these ants overwinter, and the lowest long-term tolerable temperatures is at least 5 °C, and in some localities as great as 15–20 °C. Such a considerable reserve of cold-hardiness ensures survival of nests of this species everywhere even during the most severe winters, with very low air temperatures and small thickness of the snow cover. The pattern of habitat distribution observed in species of this group agrees with the above-described pattern of their physiological capacities and environmental conditions: *L. acervorum* and *C. herculeanus* are found everywhere, whereas *L. muscorum* colonizes dry steppe areas, particularly cold in winter.

The distribution of the second species group, *F. gagatoides, M. kamtschatica* and *M. bicolor*, depends to a greater extent on the temperature conditions of the cold season. Their lowest tolerable temperatures are around –25 °C, which is close to soil temperatures observed in many localities. The overwintering chambers of these species are, therefore, positioned deeper, at 10–15 cm. This positioning of their overwintering chambers ensures the preservation of reserve cold-hardiness and allows ants of this group to overwinter almost everywhere in the sparse forest belt. Only during the most unfavourable winters soil temperatures in some areas of sparse forests reach values close to the lowest tolerable for ants. All that was said about this species group is quite true of *F. gagatoides*, which is extremely widely distributed in the sparse forest belt. However, ants of this group do not colonize most biotopes of the mountain tundra. Both *Myrmica* species occur locally, reflecting their requirements for summer, not winter conditions.

The habitat distribution of the third group, which includes four of the five species of *Formica*, is entirely limited by the temperature conditions of their overwintering. The existence of these species is possible only in areas with abnormally high temperatures of the upper horizons of the soil, or in the rare areas quickly and deeply thawing in spring and not flooded in autumn, where overwintering chambers can be positioned at considerable depths and temperatures are also relatively high. However, even in these warmest areas the difference between the lowest temperatures in winter chambers and the lowest tolerable temperatures is only 2–3 °C, and probably rather often there is no difference at all.

It should be taken into account that the data presented above refer to established ("mature") ant nests, for which the notions of building behaviour stereotypes, cold-hardiness "reserve" etc. were developed. The situation with young nests is fundamentally different. Dispersing females of all species that left their parent nests are found by the end of summer in virtually every kind of biotopes, where they start building new nests. By the beginning of winter these females have enough time to dig only a few centimetres into the soil. Thus, the overwhelming majority of them freeze to death during their very first winter, whereas most of those that survive, but colonized biotopes with temperature

conditions unfavourable for their species, die out during the next extremely cold winter. In other words, overwintering conditions have especially severe effect on young nest in particular, and this mechanism is responsible for the observed habitat distribution of ants.

In the mountain tundra, only *L. acervorum* and *C. herculeanus* are not limited in their distribution by winter temperatures. However, the latter species is connected with trees and reaches higher than 1000 m above sea level only along south-facing slopes, following the Siberian dwarf pine. Isolated nests of *L. acervorum* occur until the altitude of 1200 m above sea level on eastern and western slopes and 1400 m on south-facing slopes. In addition to these two species, *F. exsecta* and *F. gagatoides* are found on south-facing slopes, where snow cover is always thick, and soil temperatures at the depth of 20 cm are, therefore, relatively high (−15 to −18 °C), until the altitude of around 1200 m above sea level.

Thus, of the 10 ant species abundant in the Northeast of Asia, three are virtually not limited by winter temperatures in their habitat distribution, three are partly limited, and four are limited entirely.

IS THE GEOGRAPHICAL DISTRIBUTION OF ANTS LIMITED BY THEIR OVERWINTERING CONDITIONS?

These data on the connection between cold-hardiness and habitat distribution of the studied species lead to some conclusions on the dependence of the geographical distribution of ants on cold-hardiness. As noted above, the ant faunas of the Oymyakon and the Nera depressions of northeastern Yakutia are strongly depleted even compared to that of the Kolyma basin. Is winter resistance to cold related to this depletion of the fauna of northeastern Yakutia, as well as to the absence of ants in zonal tundras? To answer this question, we have to overview the general pattern of winter soil temperatures not only of the Northeast, but also of the East of Asia. Unfortunately, the available data on winter soil temperatures under natural snow cover at all the depths where ants winter are insufficient for discussing the success of overwintering in different ant species. Therefore, let us first describe the distribution of average monthly soil temperatures at the depth of 40 cm in the Northeast of Asia and then the distribution of lowest temperatures at the depth of 2–3 cm in throughout Russia.

The Upper Kolyma is a border area, influenced by both the northern branch of the Siberian High (from the west) and the deepest cyclones coming from the coast of the Sea of Okhotsk (from the south and south-west). The continentality of climate increases considerably westward of the study area, especially in the cold season, with decreasing average monthly air temperatures and annual

minimum values. In the basins of the upper and middle reaches of the Indigirka and the Yana, different meteorological stations claim the title of the "Pole of Cold" of the Northern Hemisphere, depending on the winter position of the centre of the northern branch of the Siberian High (Spravochnik..., 1966). For instance, in the Oymyakon depression (according to the meteorological station of the same name) the long-term average temperature of January is −49.5°C, while in the upper reaches of the Kolyma, Bokhapcha Meteorological Station, it is −37.9°C, with average annual minimum −64 and −53 °C, respectively.

By contrast, eastward of the Upper Kolyma, average air temperatures of January gradually increase. Snow cover thickness decreases farther from the Upper Kolyma both in towards the Pacific Ocean and westward, towards central areas of the continent (Fig. 60). Snow cover thickness in the coldest months is 1.3–1.5 times greater at the Kolyma than at the Indigirka (40–50 and 30 cm, respectively). The density of snow is low in the continental part of the area and increases to 0.20–0.25 g/cm³ near the coast.

The combined effect of these courses of air temperature and snow cover thickness distribution is reflected in the soil-temperature zoning of the Northeast of Asia (Mikhailov, 1982). Fig. 61 and Table 22 show that among large areas the lowest average soil temperatures at the depth of 40 cm in the coldest
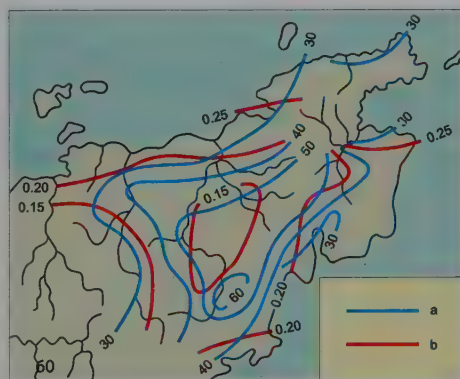
Fig. 60. Isolines of average long-term parameters of the snow cover of the second 10 days of January, according to data from 83 stations (Mikhailov, 1982). a, depth, cm; b, density, g/cm³.
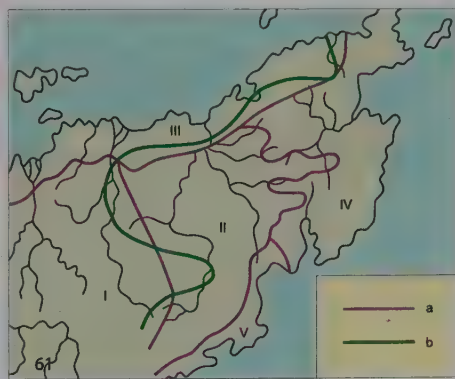
Fig. 61. Soil-temperature geographical zoning of the Northeast of Asia (Mikhailov, 1982). Regions: I, Western continental; II, Eastern continental; III, Arctic; IV, Beringian; V, Okhotsk; A, region boundaries; B, geoisotherm, −7°, from S. V. Tomirdiaro (1970). Borders between the Eastern continental and the Arctic and Beringian regions are shown according to N. K. Klyukin (1970).

month are observed in the basins of the Yana and the Indigirka (−22.2 °C); the average temperature at this depth in the Eastern continental region is considerably higher (−13.6 °C). Average values of this parameter are similar in the Arctic (−14.6 °C) and Beringian regions (−14.7 °C), reaching as high as −9.4 °C in the Okhotsk region (Mikhailov, 1982). Of course, as noted above, soil temperatures measured at meteorological stations can never describe the entire diversity of temperature conditions in the soils of particular regions. These temperatures, however, can be used for comparing regions with each other.

Our study area belongs to the Eastern continental region, and the differences between this region and the Western one are so great that they hardly require statistical testing. It is enough to note that the highest value of average monthly soil temperature in the Western continental region (−18.1 °C) is lower than the lowest value of this parameter in the Eastern region (−16.6 °C). Data on soil temperatures at the depth of 20 cm obtained at meteorological stations of the Western and the Eastern regions confirm the zoning based on temperatures at 40 cm (Table 22). Thus, the wintering conditions in the basins of the upper reaches of the Indigirka and the Yana can be considered the most severe in the Northern Hemisphere.

Table 22. Lowest average monthly temperatures (°C) of soil and months of their registration (Spravochnik…, 1966)

Region	Meteorological station	Depth 20 cm			Depth 40 cm		
		lowest temperature	month	regional average	lowest temperature	month	regional average
Western continental	Delyankir	−20.2	I		−18.1	II	
	Predporozhnaya	−25.6	II	−24.8	−24.3	II	−22.2
	Susuman	−26.4	I		−23.1	I	
	Arkagala	−27.1	I		−23.5	I	
Eastern continental	Markovo	−9.9	III		−8.6	III	
	Kanyon	−10.9	I		−9.5	I	
	Kolymskaya Stokovaya	−11.2	II		−10.9	III	
	Srednekolymsk	−14.7	II		−12.6	III	
	Zyryanka	−16.5	II	−15.2	−15.7	II	−13.6
	Elgen	−17.7	I		−15.6	I	
	Ostrovnoye	−17.9	I		−16.6	I	
	Omsukchan	−18.6	II		−16.6	II	
	Omolon	−19.3	I		−16	I	

Ant faunas change in accordance with the above-described climatic pattern. Species of the genus *Formica*, except *F. gagatoides*, *F. candida* and probably *F. fusca*, gradually disappear from the Upper Kolyma towards the Upper Indigirka. Since these two areas are both remote from the ocean and lie at the same latitude, differences between their faunas are determined not by summer heat, but exclusively by winter conditions (it is well known that in continental areas summer is considerably warmer, compared to maritime areas). At the Kolyma, the cold-hardiness reserve of *Formica* species (except *F. gagatoides* and *F. candida*) is small, only 2–3 °C. At the Indigirka, where average soil temperatures in comparable habitats are 5-8 °C lower, this cold-hardiness reserve disappears, and these species are absent.

To estimate the role of winter temperatures in the geographical distribution of ants outside the studied area of the Northeast of Asia, let us consider the distribution pattern (Fig. 62) of lowest temperatures at the depth of 3 cm in northern Eurasia (Alfimov, 2005; Alfimov & Berman, 2006). This pattern shows that the lowest soil temperatures under snow cover with thickness average for the area are no different in most of central Yakutia from those of the upper reaches of the Kolyma. However, the ant fauna of central Yakutia contains at least 24
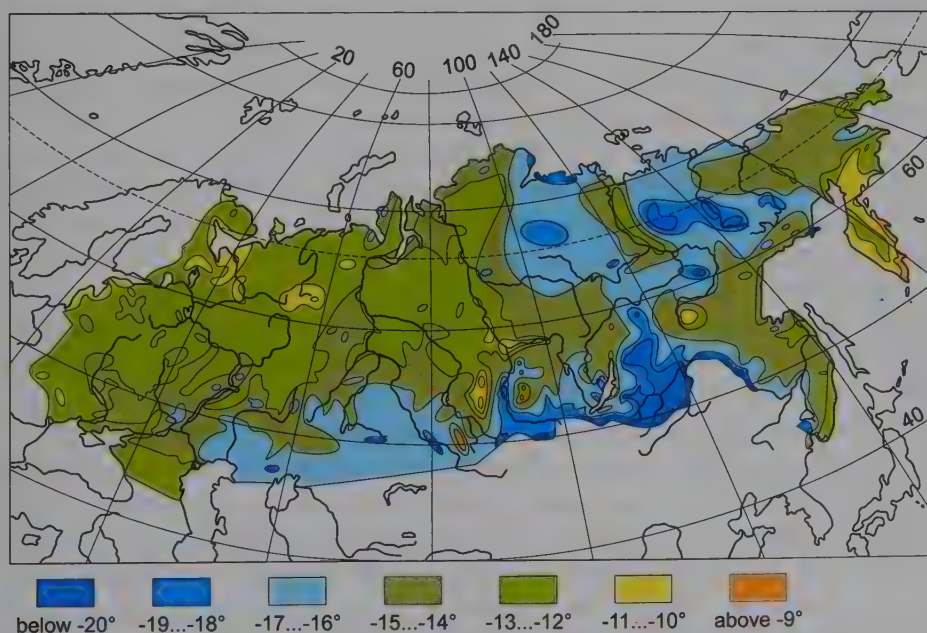

below -20° -19...-18° -17...-16° -15...-14° -13...-12° -11...-10° above -9°

Fig. 62. Distribution of average absolute minima of temperatures at the depth of 3 cm (from Alfimov, 2005; Alfimov & Berman, 2006).

species (Dmitrienko & Petrenko, 1976), i.e. 10 and 14 more than the faunas of the Kolyma and the Indigirka basins, respectively. The number of *Formica* species in central Yakutia is 14, compared to 9 in the Magadan Region (see Table 2). The causes of the higher number of species in the fauna of central Yakutia are manifold. They include the history of this region, which retained its contact with southern formations, its greater diversity of landscapes (including pine forests, steppes and some other plant communities absent in our study area) and, finally, its higher sums of positive air temperatures, 25–30% higher in Yakutsk than in the Upper Kolyma basin. The average air temperature of January is almost 6 °C higher in Yakutsk than in Oymyakon, while the lowest soil temperatures at the depth of 20–40 cm are no lower than −15...−18 °C, which is even higher than in the upper reaches of the Kolyma.

While the abrupt depletion of ant fauna from the upper reaches of the Kolyma to the upper reaches of the Indigirka and probably the Yana apparently reflects the growing harshness of winter conditions, the geographical distribution of many species to the north and northeast is limited by the decreasing summer heat supply. Let us recall that only *L. acervorum* reaches to the northern boundary of shrub tundras. Developed nests of *L. acervorum* are found in this zone only on dry and warm edges of floodplain terraces and moraines in mountain tundras pushing into the tundra zone, at a considerable distance from the boundary of long-boled forests (see below). The ultimate result of this trend is the total absence of ants in the zonal tundras of Eurasia (Chernov, 1978; Dlussky, 1967; Berman, 2001). The situation in the tundras of Alaska is similar (Berman & Zhigulskaya, 2001).

Meanwhile, the tundras of Chukotka lie between the January isotherms of −17 °C (Provideniya Meteorological Station) and −31.5 °C (Chaun Meteorological Station); snow cover thickness is only slightly smaller in Chukotka than in the upper reaches of the Kolyma. Thus, the lowest soil temperatures in zonal tundras, as Fig. 62 shows, are more or less the same as those of the Upper Kolyma basin and 6–7 °C higher than those of the Upper Indigirka basin. Since *C. herculeanus*, *L. acervorum* and *F. gagatoides* are widely distributed in the upper reaches of the Indigirka (area of the Northern Hemisphere with driest possible winters), the absence of these ants in the tundra zone is probably determined by summer conditions.

Similar reasoning can be used to explain the absence of ants in mountain tundras, where both air temperatures and, the more so, soil temperatures under snowdrifts are considerably higher than in the Kolyma valley (see Chapter 1).

To what extent are these conclusions on the dependence of the distribution of ants on the distribution of winter soil temperatures applicable to other regions? As Fig. 62 shows, areas with the lowest temperatures of the upper 3 cm of soil are found in northeastern Yakutia and Transbaikalia; in the Altai

and Tuva the lowest temperatures of this layer are in no way higher than in the Upper Kolyma basin (Alfimov & Berman, 2006). However, in the south, in the absence of permafrost, ant species that build their nests deep underground are able to exist, and such nests provide them with comfortable overwintering conditions virtually independent of temperatures in the upper layers of soil. This results in greater diversity and abundance of ants. For instance, mountain steppes of the Kuray depression (southeastern Altai), in spite of low temperatures of surface soil layers (–18 to –19 °C), are totally dominated by ants of several genera (120–140 individuals per m²), making up 50–73% of the soil macrofauna (its total density being 164–270 individuals per m² (Berman, 2001).

<p style="text-align:center">* * *</p>

The distribution of two ant species of the hypoarctic complex, *C. herculeanus* and *F. gagatoides*, reaching farther north than other ant species (except *L. acervorum*), as well as of some *Myrmica* species, has not been sufficiently studied at the southern boundary of the forest-tundra. The impression is that their distribution does not depend on small-leaved trees and is probably limited by the northern boundary of the larch *Larix cajanderi* and pre-tundra communities of the Siberian dwarf pine. The presence of coniferous trees is important to *C. herculeanus*, because, as noted above, it never build its nests in the wood of small-leaved trees. As for *F. gagatoides* and *Myrmica* species, their northern boundary coincides with that of the larch probably due to climatic factors. These ants are absent in the northern part of the Anadyr basin, where alder (*Alnus hirsuta*), chosenia (*Chosenia arbutifolia*) and birch (*Betula platyphylla*) reach much farther north than the larch (Vaskovsky, 1958; Yurtsev et al., 1985; our data). However, there is a remarkable exception still farther north (67°5' N, 178°7' W): a poplar-chosenia forest in the valley of the Telekay River (tributary of the Ekitiki, left-hand tributary of the Amguema), where Yu. P. Kozhevnikov (1974) found "black ants" (most probably, *F. gagatoides*). Along the right bank of the Kolyma the northern boundary of sparse larch forests and Siberian dwarf pines, which coincides with the northern boundary of the range of the hypoarctic complex, lies only a few dozen kilometres short of the mouth (around 69° N).

While the northern boundary of *Formica* species is probably determined by insufficient amounts of heat for completing the cycle from egg to egg in one season, the northern distribution of *Leptothorax* species is not limited by this factor, since ants of this genus are capable of prolonging their development to several years. It seems likely that their distribution is limited by the unfavourable combination of duration of ontogeny and individual life: the development of a worker ant may require more time than its life span. This hypothesis can be tested by marking larvae and adults and subsequently observing them over several years.

ON THE POSSIBLE ROLE OF BIOTIC RELATIONSHIPS IN DEPLETION OF ANT FAUNA

The preceding sections should not create the impression that the ant fauna of the Northeast of Asia is depleted exclusively because of the insufficient cold-hardiness of ants. The role of biotic relationships, for obvious reasons not included in the objective of this book, cannot be ignored. Let us note only a few points.

The impact of vertebrate animals on ants in the study area is clearly rather small. The Black Woodpecker is not abundant, and among ants it feeds primarily on *Camponotus*, as in all other parts of its range. Apparently, bears also do little harm to ants, especially those that build no piled-up domes. Little is known of damage caused by invertebrates. Myrmecophilous rove beetles, rather often conspicuously numerous in nests of *F. exsecta*, probably influence the abundance of ants.

It is more probable that ants can be affected by the general decrease of invertebrate diversity, reflected in reduced food resources, lower predation pressure, weaker competition with other ant species, etc.

Reduced food resources are probably the cause of the absence of *F. aquilonia* and *F. lugubris* in continental areas of the Northeast of Asia. Meanwhile, these species are quite common on the coast of the Sea of Okhotsk, where the heat supply of the soils of many biotopes is lower than in the Upper Kolyma basin. It has been shown that the cold-hardiness of these species is quite comparable to that of *F. exsecta*, and thus sufficient for colonizing continental areas (Berman & Zhigulskaya, 1995a, 1995b). We believe that *F. aquilonia* and *F. lugubris* are absent at the Upper Kolyma because they are unable to provide the brood of their enormous families with protein. The absence of *F. uralensis*, common in central Yakutia (Dmitrienko & Petrenko, 1976), from the basins of the Yana, the Indigirka and the Kolyma is probably caused by the same factor.

The likelihood of weaker competition is supported by the low number of ant species in communities. The number of co-existing ant species is usually no more than four; only one of the many dozens of examined biotopes had two species, *F. exsecta* and *F. sanguinea*, in addition to the hypoarctic trio; usually only one outsider species is added to this complex. It is likely that in this area, near the boundary of range for most species, some of them have their "ecological, or biotic, optimum" (Arnoldi, 1957), i.e. conditions favourable in food supply, low number of predators and weaker competition. This "biotic optimum" probably explains the huge abundance of *L. acervorum* in our study area.

In the low number of species in ant communities of the Northeast of Asia we see also the main factor responsible for the amazing range of *F. gagatoides*,

reportedly (Dlussky, 1967) lying north of the 60th latitude (except in mountain systems, by which this species reaches far south). It is clear that the hydrothermal conditions south of the 60th latitude are no less suitable for *F. gagatoides*, but in these areas the abundance of a large group of *Formica* species widely distributed in the Palaearctic considerably increases, probably determining the absence of this species in middle and southern taiga.

Evidence of the low competitive capacity of *F. gagatoides* is probably provided by its spatial relationship with *F. lemani* in various parts of the Northeast of Asia. As noted above, the extreme winter conditions and the continuous permafrost strictly limit the habitat distribution of *F. lemani* in continental areas, where this species is confined exclusively to dry south-facing slopes, rare in this region. In maritime areas (near Magadan), due to the localisation of permafrost mostly in lower parts of the relief, *F. lemani* is dominant even in mesophyte communities; *F. gagatoides* is suppressed in most habitats suitable for its existence and preserved chiefly in waterlogged areas, which *F. lemani* cannot colonize because of permafrost (Photo 47, 48). The impression is that the habitat and geographical distribution of *F. gagatoides* (except the northern boundary of its range) is determined by interspecific relationships, whereas the distribution of *F. lemani* is determined by wintering conditions.

We may also hypothesise about the antagonistic relationship between *F. gagatoides* and *F. candida*. *F. candida*, a species with extremely high ecological valence, in southern part of its range inhabits a huge range of biotopes, from wetlands to dry steppes on sandy soils (Zhigulskaya, 1975). However, in more western parts of the range it is driven out by ants of the *F. rufibarbis* group into wetlands, where these species are virtually absent, while *F. candida*, with its habitat versatility and nest-building plasticity, is able to exist (Dlussky, 1967). At the Kolyma *F. candida* is preserved mostly in floodplain areas, where no other ant species, except *M. bicolor*, is able to live, because of regular flooding at high waters. Unable to withstand the pressure of cold (or suppressed by decreased soil temperatures, probably, as hypothesised above, catastrophic to this species as well as to *F. exsecta*), *F. candida* left its place in zonal communities free to be occupied by *F. gagatoides*.

If the hypothesis about the possible increase in the abundance of *F. candida* (as well as *F. exsecta*) after it was ruined by long-term climatic fluctuations is true, it can be expected that the abundance of the weaker competitor *F. gagatoides* will be simultaneously decreasing. Decreasing abundance of *F. gagatoides* in many biotopes will lead to considerable changes of the pattern of habitat distribution we have described. To test this hypothesis, careful censuses of ants should be carried out again along the basic transects at the Aborigen Field Station, encompassing the principal diversity of biotopes of the study area.

Photo 47. Tussocky sedge–cotton-grass wetland at the time of fructification. Such biotopes are usually not inhabited by ants. But at their edges, closer to the forest, cones of *F. exsecta* are sometimes found, using tussocks as foundation.

Photo 48. Forest tundra at the coast of the Sea of Okhotsk. In tundra areas ants are absent, but in every clump the hypoarctic species and *F. exsecta* are abundant.

Finally, we have to mention the absence of *L. muscorum* in the Northeast of Asia, except in steppe areas of eastern Yakutia and pine forests of the environs of Okhotsk (see Chapter 2). This species, with its record cold-hardiness, is undoubtedly broadly mesophilic, and thus its absence in mesophyte communities of the Northeast of Asia can be determined neither by lack of heat in summer, nor by too low temperatures in winter, nor by biotic relationships. Probably we deal here with a peculiar relict xerophile form preserved in these areas, which is morphologically indistinguishable from *L. muscorum*.

CONCLUSIONS

• Ants of continental mountain forests of the Northeast of Asia confirm the reputation of this region as an area with extremely harsh climate: ant species diversity decreases by the factor of at least 4.5 times from south to north. There are about 80 species of ants in the Primorye and the Amur Region (Kupianskaya, 1990), but in the Northeast of Asia, including the Indigirka basin, we found only 18 species, mostly trans–Palaearctic. Only three species (*L. acervorum, C. herculeanus* and *F. gagatoides*) are extremely abundant, inhabiting virtually the whole diversity of biotopes, including zonal ones. Ten species are relatively abundant, but located in small habitats, with conditions sharply deviating from background conditions of the region. The remaining species are so rare that their habitat distribution is not clear.

In open thinned forest stands, typical of the taiga zone of the Northeast of Asia, the community structure of the invertebrates of soil macrofauna as a whole and dominant ant species in particular is almost entirely dependent on relief through the following chain: "location—drainage—type of permafrost (icebearing or "dry")—heat supply—soil vegetation cover—ant population". An important part can be played by the reduction of insolation by the cover of forest canopy. Most of the area is covered by cold and wet biotopes with ice-bearing permafrost and thin seasonally thawed layer, therefore almost everywhere dominated by a community of centipedes (two or three species) and mesophyllic ants (three or four species). In other words, in the community of soil macrofauna, which occupies the huge areas, the obligate and facultative predators feeding on members of mesofauna are extremely numerous in lax peat. Thus, ants occupy an extremely important place in the soil macrofauna population in the belt of sparse forests in the Upper Kolyma basin.

• The three above–mentioned species are perfectly adapted both to the summer conditions, rather poor in heat, and to the winter colds of this area. These species colonize even north-facing slopes, where sunshine duration is very low, until the altitudes of around 1100 m above sea level, which shows how well they are adapted to summer conditions. The overwintering chambers of *L. acervorum* and *C. herculeanus* are usually positioned no deeper than 10 cm, where the low-

est temperatures reach −25° to −28 °C, showing their independence of winter conditions; moreover, each winter these ants endure temperatures lower than −20 °C for almost two months. However, not these three species, but *L. muscorum*, is an example of truly phenomenal adaptation to such conditions. This species, found in adjacent areas of northeastern Yakutia, lives in winter under even lower air temperatures: averages absolute temperature minima are −59 to −61 °C. In summer, sites inhabited by *L. muscorum* are not only the warmest (highest temperatures at the depth of 10 cm are around 25–28 °C) in all the studied biotopes of the region, but also the driest (water content is about 2–5%, i.e. close to the limit of precision provided by the gravimetric method). Thus, *L. muscorum* is adapted both to the winter colds and to the summer heat, as well as to the dryness of the substrate all the year round.

F. gagatoides, together with *M. kamtschatica*, unlike the above-mentioned species, winter somewhat deeper, in the layer at the depth of 10–15 cm, rarely 25 cm, where they are exposed for up to one month to temperatures lower than −15 °C, with lowest values reaching around −18 to −22 °C. The overwintering chambers of the other species are located either deeper (up to 1.5 m), or close to the surface, but in specific habitats; in any case, the temperatures in the nests of all of these species never fall below −10 to −13 °C.

• The overwhelming majority of the studied ant species keep strictly to their peculiar stereotype of nest organization. We never found nests of *C. herculeanus* or *Leptothorax* spp. with deeply positioned chambers or, on the contrary, the nests of *F. exsecta*, *F. candida*, *F. lemani* with surface position of overwintering chambers, even in places with temperatures sufficient for successful overwintering. Due to their ability to move actively at slightly sub-zero temperatures, *Formica* spp. can shift downwards along the tunnels of the nests, and thus their vertical distribution in the nest is determined by autumn temperatures.

However, in spite of preserving their nesting stereotypes, some species in the Northeast of Asia clearly change the type of their habitat distribution. *F. candida*, a eurytopic species in southern Siberia, in the Kolyma area inhabits, as we have observed, virtually exclusively sandy-pebbly parts of river floodplains, i.e. uses only one habitat type of the many it colonizes in other parts of its range. The range of habitats of *F. exsecta* in the Northeast of Asia is narrowed: it successfully overwinters in particularly warm areas in valleys, or at the upper boundary of the forest. Since there are not many habitats peculiar to the mentioned two species (and to *F. lemani* as well), the total area occupied by these species is rather small.

• Permafrost, developed virtually everywhere in the region (except talik zones along rivers), can prevent the positioning of overwintering chambers at depths

with temperature conditions suitable for overwintering. The influence of permafrost in areas with thin thawed layer directly affect the temperatures and the water content even of the uppermost soil horizons. In these horizons very strong temperature gradients (up to 2.5 °C per cm) are formed, which, together with the high position of the permafrost table, and as a result of high water content, determine the greatest possible depth of the position of tunnels and chambers. Such a situation with permafrost is characteristic of the region as a whole, but it is most vividly expressed on north-facing slopes, and also virtually always on the lower, waterlogged parts (trains) of all slopes, in saddles, as well as at bottoms of valleys.

Permafrost does not visibly influence the hydrothermal regime of the upper soil layers in deeply and quickly thawing areas, and, consequently, does not affect the ecology of the inhabiting species, especially those that build their nests close to the surface. None of the species of *Formica*, except *F. gagatoides*, normally inhabits biotopes with thin thawed layer, because they have little cold-hardiness and locate their overwintering chambers far below the surface. Colonies of *F. exsecta*, however, sometimes occur in such biotopes, but only with unusually favourable combinations of the principal factors (abundance of snow, location in the upper part of the belt with relatively high air temperatures, etc.). *F. lemani* has never been found in areas with permafrost of high ice content, which serves as a limiting factor for its distribution; but at the coast of the Sea of Okhotsk, with its discontinuous permafrost, this species is quite widespread.

• All the studied ants overwinter not in the frozen, but in the supercooled state. The lowest supercooling point is recorded in *L. muscorum* larvae (−58.1 °C), and this value can be considered a record for ants as a whole. The temperature range of supercooling points is −38 to −43 °C in *L. acervorum*, −37 to −44 °C in *L. muscorum*, −37 to −40 °C in *C. herculeanus*, −27 to −30 °C in *F. gagatoides*, −27 to −31 °C in *M. kamtschatica* and *M. bicolor*, −24 to −25 °C in *F. candida*, −20 to −24 °C in *F. lemani*, −19 to −22 °C in *F. exsecta*, and −17 to −18 °C in *F. sanguinea*. The lower lethal temperature ($LT_{50\%}$) of all the species is around 3–7 °C higher than their average values of supercooling point.

The above-listed cold-hardiness parameters of ant species are noticeably greater than those found in other regions with milder climate. For instance, in southern and northern Finland, and even in the environs of Magadan, average winter cold-hardiness parameters of each of the studied species of *Formica* are very close to their summer values in ants from the Aborigen Station. But similar winter temperature conditions and even milder ones are characteristic of most of the area of Russia, except regions with continental climate, determined by the Siberian High. It remains yet to be found to what extent the cold-hardiness of

ants increases from summer to winter in the above-mentioned areas, compared to the Aborigen Station.

The main difference between the wintering state of the ants we have studied in the Upper Kolyma basin and those wintering in non-permafrost regions is that in the Northeast of Asia ants are physically supercooled, i.e. they remain "liquid" under temperatures below the freezing point. This state is rather stable, and all the species of *Formica* remain supercooled at least for several months; other species (which significantly decrease their freezing point) remain in this state for some weeks during the periods of lowest air temperatures. As a rule, in regions with seasonally frozen ground, temperatures in overwintering chambers are not only above the supercooling points of ants, but also above their freezing points.

• The occurrence of a species in a particular area suggests that the species is adapted to the conditions of this area. "Reserve of cold-hardiness", which we define as the difference between the lower lethal temperature and minimal temperatures in the nests, can serve as a measure of adaptation to local conditions. The greater this difference, the greater the resistance of a species to the vicissitudes of winter weather, and the greater the range of biotopes it can inhabit. The reserve of cold-hardiness is particularly great in *L. muscorum, L. acervorum* and *C. herculeanus*. It amounts to 10–15 °C and guarantees the safety of the populations of these species almost everywhere, even during cold winters and winters with thin snow cover. *F. gagatoides, M. kamtschatica* and *M. bicolor* have only half of this reserve, 5–7 °C, which is, nevertheless, enough for a very broad geographical expansion to the Hypoarctic belt and for the broad habitat distribution of *F. gagatoides* even in the coldest regions. The two other above-mentioned species have narrower habitat distributions, limited by summer conditions. Four species of the genus *Formica* (*F. exsecta, F. candida, F. sanguinea* and *F. lemani*) have the lowest cold-hardiness, their reserve not exceeding 2–3 °C, and completely disappearing during unfavourable years; accordingly, all these species occur locally in our study area.

• *F. gagatoides* appears to be the most adapted of all the *Formica* species (judging by the value of its cold-hardiness reserve) to the conditions of the general zonal biotopes, which are cold all the year round, and besides are damp (moist) in summer. It is able to build primitive nests with wintering chambers close to the surface. The degree of adaptation to the winter cold in *F. gagatoides* is close to that of the champions of cold-resistance, *C. herculeanus* and the two species of the genus *Leptothorax*. In this connection (and not only because of its geographic range configuration) *F. gagatoides* well deserves its Russian name *polyarny muravey* (the polar ant).

The summer adaptive capacity of *F. gagatoides* is considerably restricted, compared to that of the two other background species, as well as that of *M. kamtschatica*. Not only is the cold-hardiness of this species greater than or comparable to that of *F. gagatoides*: they are also able to prolong their development to several years. As for *F. gagatoides*, it is an "annual" insect: its ontogeny lasts one year, since its brood is unable to survive the winter. The more amazing it is that, in spite of these disadvantages, *F. gagatoides* belong to the group of dominant species, and all of them (*C. herculeanus, F. gagatoides* and *L. acervorum*), due to their wonderful adaptability, are very widely distributed in the Hypoarctic, and can be considered attributes of the Hypoarctic as much as crowberry, Labrador tea, dwarf birch etc.

• The studied species are divided into two groups according to their biochemical mechanisms of cold-resistance and the seasonal changes of their temperature parameters. Ants of the first group (*L. acervorum, L. muscorum, C. herculeanus, M. kamtschatica* and *M. bicolor*) have supercooling points changing considerably from summer to winter, at most by 25–30 °C (mostly because of the decrease of the freezing point); their cryoprotection mechanism is based on the accumulation of polyols (10–20%). It is remarkable that the larvae of all the species of this group are overwintering (in contrast to adults only in Group II), although they have very soft chitin exoskeletons. In spite of the very low temperatures of overwintering, neither larvae nor adults dry out. Apparently, the type of exoskeleton in this case is not crucial for dehydration avoidance in ants (as well as in many other insects).

In the second (species of the genus *Formica*), supercooling points decrease from summer to winter by only 6–12 °C; freezing points decrease by 1–6 °C; polyol content is rather low (0.4–2%), but the concentration of sugars increases (3–6%). Thus, the biochemical foundation of cold-hardiness is determined mainly at the level of genus and higher taxa. However, generic or even subgeneric characteristics of the studied insect group determine the adaptive strategy of cold-resistance of particular species far from completely. *F. lemani, F. candida* and *F. gagatoides*, members of the same subgenus (*Serviformica*), in the Upper Kolyma basin inhabit biotopes atypical for this genus (Chernov, 1988). But these species have, nevertheless, extremely different parameters of cold-hardiness. It is rather "average" in *F. lemani* and *F. candida* (compared to the entire cold-hardiness range of the studied species), but the resistance of *F. gagatoides* to cold is so high that it proves to be close to that of the genus *Myrmica*, in which it is based on other biochemical pathways. Thus, similar degrees of cold-hardiness are achieved by different biochemical methods.

• The adaptive strategies of the studied species are not only determined by their physiological and biochemical capacities, but realized through different

combinations of physiological, biochemical and behavioural mechanisms. Very broadly one can distinguish three groups with different adaptive solutions to the problem of low wintering temperatures; these very groups embody different limits of habitat distribution. Ants of Group I (*L. acervorum, L. muscorum* and *C. herculeanus*) use mostly their physiological/biochemical resources: extremely high resistance to cold lets them hibernate at the very surface of the soil in an overwhelming majority of biotopes. In Group II (*F. gagatoides, M. kamtschatica* and *M. bicolor*) adaptation to cold is based on behaviour compensation for the lack of physiological/biochemical resources, i.e. choosing localities for nest-building where the overwintering chambers can be positioned in the soil at sufficient depth. Group III, which includes the species most sensitive to cold, exists only in special, favourable conditions, which are formed in a small set of habitats; the physiological/biochemical capacities of this group are limited.

The mixed composition of Group II (it includes members of two different genera) and the diversity of cold-resistance in the outsider group show that the adaptive strategy of species can be individual and not be determined by genus (in this connection it seems correct to consider individual "tactics"). But the integrated adaptive effect of different tactics used by different species, which can be estimated, for example, by the density of nests and the range of inhabited biotopes, in a number of cases appears to be virtually the same. The most striking examples—the key species for understanding the strategies of adaptation to cold—are *F. gagatoides*, which appears to be omnipresent in our study area, and two other hypoarctic species, *L. acervorum* and *C. herculeanus*, equally omnipresent.

The demonstrated individuality of adaptive tactics found in studied species leaves little hope that a common strategy of adaptation to cold (including physiological/biochemical and behavioural aspects) will ever be discovered, at least in ants.

• To what degree do ants of the Upper Kolyma area realize their potential of cold-resistance? The observed cold-hardiness parameters of most species seem to be close to the extreme possible in ants. Their geographical distribution gives indirect evidence to this conclusion: the ant fauna of "the Pole of Cold" area is considerably depleted, compared to that of the Upper Kolyma area and, even more so, to that of central Yakutia. More severe winter conditions of northeastern Yakutia, compared to the other mentioned regions, proves to be intolerable to many species of the genus *Formica* and, possibly, also of the genus *Myrmica*.

Extreme low temperatures of surface horizons of the soil are not an exclusive property of northern regions. There is a second "Pole of Soil Cold" in southern parts of Central and East Siberia; the first one coincides with the Pole of Cold for air temperatures, located in northeastern Yakutia. In Tuva, Transbai-

kalia and in the Upper Amur valley the surface horizons of the soil are cooled almost as much as in Oymyakon, not because of extremely low air temperatures (higher in this area than in the Oymyakon depression), but rather because of the almost complete absence of snow cover: the amounts of snow falling in this area are small, and the snow that falls is blown away (Alfimov & Berman, 2006).

However, the temperature regime of the deeper soil and ground horizons in the northern and the southern "Poles of Soil Cold" are radically different. In the north permafrost is continuous everywhere (except in talik zones), while in the south soils and ground, though freezing to depths of over 1 metre, at greater depth retain above-zero temperatures all the year round. This circumstance fundamentally changes the living conditions of the ants that build nests with deeply positioned overwintering chambers. In the northern "Pole of Soil Cold" all the members of the genus *Formica* (except *F. gagatoides*) have to take shelter in biotopes with a thick seasonally thawed layer (which occupy only a small part of the area), where they can literally bury themselves as deep as possible and thus escape the low winter temperatures. In the southern "Pole of Soil Cold" ants build ground nests everywhere deeper than the seasonally freezing layer, with overwintering chambers in horizons with temperature conditions comfortable for overwintering, and thus they are rather abundant in this area. As for the relict mountain steppes of northeastern Yakutia, where the lowest temperatures of surface horizons of the soil are comparable, ants building deep nests are totally absent, because of low winter temperatures at the level of their winter chambers as well as the extremely low water content along the entire soil profile in summer. Consequently, the northern and the southern "Poles of Soil Cold" are unequal in their ecological conditions. The rarity of the genus *Formica* in the ant fauna of the Upper Kolyma area is not directly related to the low air temperatures and insufficient cold resistance of ants themselves. In most cases it is caused by low temperatures indirectly, through the influence of ice-bearing permafrost, which makes nest-building impossible.

• The considerable similarity of the winter temperature (and permafrost) conditions of central Yakutia and the Upper Kolyma basin and considerable difference between the faunas of these areas are evidence that the limiting factor is, above all, the lack of summer heat supply. Historical factors may also play some part: in the vast area of northeastern Asia the probability of the restoration of a species that died out, e.g. following an abnormally cold winters with thin snow cover, is low, since, in contrast to central Yakutia, potential sources of a secondary invasion are remote.

The question about the degree to which ants realize their cold-resistance potential in the Northeast of Asia has some applied value as well. Chitin remains of *C. herculeanus*, *L. acervorum* and two species of the genus *Formica*

have been found in deposits of cold periods of the Late Pleistocene in several sections of northeastern Asia (Kiselev, 1981). One of the *Formica* species is undoubtedly *F. gagatoides*, the other most probably *F. candida*. These facts indicate the possibility of even greater ant cold-hardiness than we have revealed. And if experiments show that the cold-resistance of these species in the Oimyakon depression is the greatest possible, then fossilized remains of ant can be used as reliable indicators of the winter temperatures of Pleistocene landscapes.

• Summarizing, we may make an assertion that cold-hardiness is one of the most powerful factors defining the genesis of the ant fauna in the Northeast of Asia, along with, first, insufficient amounts of summer heat for successful ontogeny (which determines, e.g., the absence of the ants in zonal and mountain tundras, due to low summer temperatures), and second, historical circumstances (a striking example of its effect is *L. muscorum*, the absence of which in the Kolyma basin is definitely not temperature-related). High cold-resistance helps the hypoarctic complex of ants to survive the most severe winters throughout most of northern Eurasia, including its extracontinental parts, and to reach in their expansion the northern limits of summer conditions sufficient for completing their life cycle. In such regions as the upper reaches of the Yana and the Indigirka, with their extremely low winter temperatures, the restricted cold-hardiness of the ants of the genus *Formica* manifests itself in the depletion of their fauna even in areas lying far south of the boundary of tundra.

• Such is the role of cold-hardiness in the genesis of fauna in stable climatic conditions, i.e. observed over a relatively short period of time. Describing the wide range of biotopes inhabited by *F. exsecta* (Chapter 5), we hypothesised that the present state of its population is residual, i.e. results from the catastrophic effect of a climatic fluctuation (thin snow cover with extremely low air temperatures), which ruined in the study area most of the population of this species, which has been restoring its numbers in the recent decade. The population of *F. candida* probably also suffered from a similar catastrophe in areas outside floodplains; this could be the reason why we found only isolated nests of this species in zonal landscapes in the course of our study. The cause of these catastrophes is not necessarily related to short-scale climatic fluctuation: it may reflect changes of a larger scale, the present phase of which is commonly termed "global warming". No matter what caused the warming, the continuing restoration of the population of *F. exsecta* is a fact, apparent from the abundance of the noticeable piled-up cones of the nests of this species, even without counting the nests. Following this reasoning, we may expect similar population growth in other species of this genus, since all of them, except *F. gagatoides*, are less cold-hardy than *F. exsecta*.

● The results of our study made it clear that only a few ant species are indifferent to the pressure of the lack of summer heat and extremely low wintering temperatures, environmental factors of primary importance in the north. However, there is no doubt that biotic relationships, which remained beyond the scope of this book, also contribute to the formation of species composition, spatial distribution and abundance of ants. Hypotheses about the decreasing diversity of invertebrate communities, reflected in the lack of protein food for ant species with large families, and about the possible role of competition, require further testing by detailed special studies. In this book we only emphasized that in subarctic areas of the Northeast of Asia biotic relationships retain their role as a factor in the genesis of faunas.

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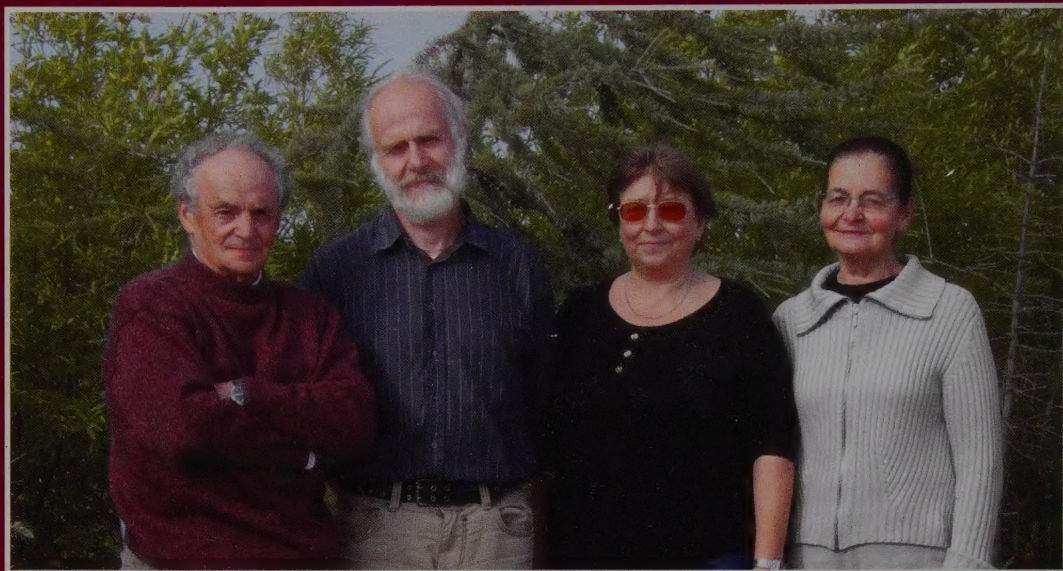
This monograph attempts to determine how land insects (several abundant species of ants taken as an example) adapt to winter survival in northeastern Russia, the region with the lowest winter temperatures in the Northern Hemisphere. Data on the geographical, landscape and habitat distribution of species, the abundance of nests and families, location and organization of nests and population structure are given. Winter thermal regimes under conditions of extreme continental climate in differently positioned nests are described in detail. The influence of permafrost on the vital functions and wintering conditions of ants is examined. Characteristics of the cold-hardiness of larvae and adults (supercooling points and long-term tolerable temperature), seasonal changes in these parameters and concentrations of substances enabling cold-hardiness are given. The summarizing part of the book contains analysis of the relations between spatial distribution and cold-hardiness in ants in general, as well as of the adaptive strategies of these insects, which are intolerant of tissue freezing, that enable them to exist under extremely harsh climatic conditions.

The book is addressed not only to entomologists working in biological and agricultural research institutes, but also to all ecologists interested in the strategies of animal adaptations to extreme conditions and cold in particular. The book will also be of use to students of biology and of local lore.

"This excellent monograph brings together the results of fundamental, field-based studies on ants in north eastern Asia undertaken over 30 years of research collaboration by a group of researchers in the Magadan Region."

Dr William Block,
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